

On the confusion surrounding *Pareledone charcoti* (Joubin, 1905) (Cephalopoda: Octopodidae): endemic radiation in the Southern Ocean

A. L. ALLCOCK FLS*

Marine Systems Research Group, School of Biology and Biochemistry, Queen's University Belfast, 97 Lisburn Road, Belfast BT9 7BL, UK

Received September 2003; accepted for publication July 2004

Until recently, all papillated specimens of *Pareledone* were ascribed to the species *Pareledone charcoti* (Joubin, 1905), of which *P. aurorae* (Berry, 1917) was considered a junior synonym. Re-examination of the papillated type material of *Pareledone*, coupled with extensive fishing over several years off the Antarctic Peninsula, has led to a revision of this position. Seven new species of papillated *Pareledone* are identified from the Antarctic Peninsula region. They are identified by subtle taxonomic characters, such as the morphology and placement of their papillae, although traditional indices often fail to separate the species. Whilst apparently sympatric, there is some evidence of niche separation of these species with respect to depth. A key is provided for their identification. © 2005 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2005, 143, 75–108.

ADDITIONAL KEYWORDS: Antarctica – identification key – Mollusca – new species – Octopoda – systematics.

INTRODUCTION

The genus *Pareledone* is the most abundant and diverse octopod genus in the Antarctic (Allcock *et al.*, 2001). It is endemic to the Antarctic, with species only found south of the Polar Front. Although putative specimens have been caught further north, examination of these specimens (where available) shows these to have been misidentified. Taxonomic problems have undoubtedly arisen because of a paucity of specimens. A corollary of this is that a lack of taxonomic study has hindered other researchers who have undoubtedly lumped multiple species under only a few names (e.g. Kühl, 1988).

Octopuses are agile, have good visual acuity, and are difficult to catch in typical benthic research gears such as Agassiz trawls. In recent years, however, the Alfred Wegener Institute has conducted several research cruises aboard *RV Polarstern* to the Antarctic Peninsula and fished using commercial bottom trawls. This has provided an excellent opportunity to collect large

numbers of papillated *Pareledone*. It quickly became apparent that specimens previously ascribed to *P. charcoti* comprised a number of closely related species. Seven new species are described herein, the papillated species of *Pareledone* are reviewed and an identification key is provided.

TAXONOMIC HISTORY

The genus *Pareledone* was reviewed by Lu & Stranks (1994) following extensive fishing in eastern Antarctic waters. They concluded that of the 12 species described, two, *P. carlgreni* Thore, 1945 and *P. nigra* (Hoyle, 1910) (neither of which is found in the Southern Ocean), properly belonged in the genus *Aphrodotopus*. More recently, *P. adeliaana* (Berry, 1917), its junior synonym *P. umitakae* Taki, 1961, together with *P. polymorpha* (Robson, 1930) have also been removed from *Pareledone* (Allcock *et al.*, 2003). This leaves seven described species, three of which have smooth skin, *P. antarctica* (Thiele, 1920), *P. harrissoni* (Berry, 1917) and *P. turqueti* (Joubin, 1905) and are not dealt with in this study. Of the four papillated species, *P. framensis* Lu & Stranks, 1994 and *P. prydzensis* Lu

*E-mail: l.allcock@qub.ac.uk

& Stranks, 1994 are recently described, whilst the descriptions of *P. charcoti* (Joubin, 1905) and *P. aurorae* (Berry, 1917) date from the early part of the last century.

Pareledone charcoti is the only papillated species previously reported from the Antarctic Peninsula. It was described from a specimen found on the beach (Joubin, 1905) and has subsequently been found from shallow waters (c. 25 m) to depths of c. 700 m. It is reported to have a circum-Antarctic distribution (Lu & Stranks, 1994). Two forms of the species have been noted which differ in the shape of the papillae on the dorsal surface. Robson (1930, 1932) commented that Joubin's (1905) description dealt with a 'heavy sculpture of closely opposed boss-like tubercles' whilst his later paper (Joubin, 1914) described 'a more granular type of sculpture, the tubercles being smaller and more widely spaced'. Berry's (1917) description of *P. aurorae* is quite similar to Joubin's 1914 description of *P. charcoti* and Berry (1918) himself suggested that the former might be a junior synonym of the latter. Kubodera & Okutani (1994) conclude that 'specimens fixed while alive have distinct tubercles . . . identical to the form seen in the type of *P. charcoti*' whereas 'specimens fixed when dead . . . tend to have low, indistinct tubercles . . . found in the type of *P. aurorae*'. They concur with Berry that the two species are synonymous.

MATERIAL AND METHODS

Between 16 November and 26 December 1996 a benthic survey of the Antarctic Peninsula was undertaken by *RV Polarstern* (expedition ANTARKTIS, XIV/2; Kattner, 1998). Three gear types (commercial bottom trawl, benthopelagic trawl and Agassiz trawl) were deployed off Elephant Island, King George Island, and Adelaide Island. Recurrent problems with the net sounder meant that the benthopelagic net occasionally touched the sea floor and hence yielded benthic octopodids. A demersal finfish survey during the cruise meant that bottom trawling was extensive in depths less than 400 m. Cruise time, however, also allowed some deeper areas to be surveyed. The sampling yielded 1582 papillated specimens of *Pareledone*.

As part of expedition ANTARKTIS, XVII/3 (Arntz & Brey, 2001), *RV Polarstern* fished in the area of the Bransfield Straits and South Shetland Islands between 24 April and 7 May 2000. Specimens were collected predominantly with a commercial bottom trawl. The sampling yielded 70 papillated specimens of *Pareledone* at depths ranging from 100 to 900 m.

During expedition ANTARKTIS, XIX/3 (Fütterer, 2003), a CCAMLR fish survey was conducted in the region of Elephant Island, the continental shelf region

north and west of the southern South Shetland Islands, and the shelf north of Joinville Island. Between 29 January and 21 February 2002, a commercial bottom trawl yielded 1703 papillated specimens of *Pareledone*.

Specimens were examined live where possible and when freshly dead. A small number of specimens were preserved in 4% formalin and shipped to the UK where they have been deposited in the Natural History Museum, London (BMNH) or the National Museums of Scotland, Edinburgh (NMSZ). A map is provided of the capture locations of the specimens preserved from the three cruises outlined above (Fig. 13).

Radulae were dissected from the fixed buccal mass and tissue dissolved from around them using Milton's sterilizing solution. They were then attached to sticky carbon pads and sputter coated with a gold alloy before being examined under a high vacuum electron microscope. Two or three specimens of each species were prepared and the best preparation illustrated. Radulae appeared to show consistency in morphology within a species (hence the single illustration per species), although the height and sharpness of rachidian cusps did vary. This is unlikely to have been caused by wear since the sections of radulae photographed were from the middle of the radular tube.

Comparative material was made available by the Australian Museum, Sydney (AMS), the Museum National d'Histoire Naturelle, Paris (MNHN), the Natural History Museum, London (BMNH), the Zoologisches Museum, Berlin (ZMB) and Museum Victoria (NMV). As octopuses suffer greatly from shrinkage on fixation it is important to know whether they were measured before or after fixation. Measurements in square brackets refer to fresh material. All other measurements, including those given in the tables, are taken from formalin-fixed material. Where measurements were taken before and after fixation both figures are given to illustrate the levels of distortion. Where indices are calculated, the values given are the mean \pm standard deviation. Size descriptors (e.g. large, deep), where given alongside indices, follow the guidelines proposed at the taxonomy workshop at the Cephalopod International Advisory Council Symposium in Phuket, 2003.

Abbreviations used are those recommended in the guidelines for octopus taxonomy published by Roper & Voss (1983) and are as follows: mantle length (ML), total length (TL), mantle width index (MWI), head width index (HWI), web depth index (WDI), funnel length index (FuLI), mantle arm index (MAI), arm length index (ALI), arm sucker index (ASI), opposite arm index (OAI), ligula length index (LLI), calamus length index (CaLI), spermatophore length index (SpLI).

SYSTEMATICS

FAMILY OCTOPODIDAE ORBIGNY, 1840
PALELEDONE ROBSON, 1932

Emended diagnosis

Mantle saccular. Stylets present. Arms with uniserial row of suckers. Right third arm of males hectocotylized; copulatory organ with clearly differentiated ligula and calamus, ligula groove shallow and without marked transverse ridges; arm tips not otherwise modified. Suckers moderately large; distinct enlarged suckers absent. Web well developed. Funnel organ VV-shaped or W-shaped. Ink sac present or absent; anal flaps present or absent. Radula composed of rachidian, two pairs of unicuspid lateral teeth, a pair of unicuspid marginal teeth and a pair of marginal plates. Beak is of the classic octopodid form with rostral tip of lower beak rounded. Chromatophores absent from connective tissue covering dorsal surface of digestive gland.

Type species

Eledone charcoti Joubin, 1905. By subsequent diagnosis.

Remarks

Some studies have suggested that stylets are absent in *Pareledone* (e.g. Lu & Stranks, 1994). They are absent in *Adelieledone polymorpha* (Robson, 1932) which was placed, until recently, in *Pareledone* (Allcock *et al.*, 2003), but appear to be present in all other *Pareledone* species where they are extremely small and delicate. They may therefore easily be overlooked.

Previous descriptions of *Pareledone* have also suggested that the funnel organ may be VV-shaped or W-shaped, but usually this is because species of the genus *Adelieledone* Allcock *et al.*, 2003 (which are W-shaped) have been included in the description. During this study, perhaps because of the large number of specimens examined, there appears to be greater variation in the form of the funnel organ than was previously appreciated. It is not known how much of this variation may be attributed to fixation since the funnel organ is usually not visible prior to fixation.

The web depth index for *Pareledone* species gives the impression that the web is deep. This is not apparent on visual inspection rather than measurement and calculation. This is because of the way octopuses are measured. The arms of *Pareledone* are relatively short compared to their width, and even if there were no web, the distance from the centre of the oral surface to the edge of the brachial crown would be at least 20% of the arm length. Under the scale proposed at the CIAC 2003 taxonomy workshop this equates to 'moderate' depth (a result of 25% or greater equates to 'deep') even though the web itself (excluding the brachia) may be extremely shallow.

PALELEDONE CHARCOTI (Joubin, 1905)
 (FIGS 1A–G, 9A, 10A, 11A, TABLE 1)

Eledone charcoti Joubin, 1905: 22, pl. 3, figs 1, 2.
 Not *Eledone charcoti* – Joubin, 1914: 35, figs 1, 2. – Odhner, 1923: 6.
 Not *Graneledone charcoti* – Robson, 1930: 388.
Moschites charcoti – Hoyle, 1912: 279, text-figs 6, 7
 Not *Moschites charcoti* – Massy, 1916: 151, figs 12–21.
 Not *Moschites aurorae* Berry, 1917: 20, pl. 12, fig. 9, pl. 13, figs 10–12, text-figs 14–20.
Pareledone charcoti – Köhl, 1988: 90 [in part]. – Allcock & Piartney, 2002: 129, fig. 2. – Piatkowski, Allcock & Vecchione, 2003.
 Not *Pareledone charcoti* – Lu & Stranks, 1994: 224–226, figs 2, 9e–h. – Okutani, 1986: 279, pl. 3. – Piatkowski *et al.*, 1998: 43. – Allcock, 1997: 92, pl. 4 : 10. – Allcock *et al.*, 2001: 835.
Pareledone cf. charcoti type 2 – Piatkowski *et al.*, 1998: 43.
Pareledone sp. 16 – Allcock, 1997: 125, fig. 4.8, pl. 4.17.

Material examined

Lectotype: MNHN 5.7.1095, Ile Wandel, 65°05'S, on the shore, coll. 'Charcot' Antarctic Expedition, 3.ix.1904: 1♀ submature 32 mm ML.

Other material: NMSZ 2002037.044, *RV Polarstern*, stn 61/051–1, 31.i.2002, 61°12'S, 54°50'W, 62–94 m: 1♂ immature [31] mm ML, 8♂ mature 30 [38], 37 [38], 36 [39], 36 [40], 42 [42], 37 [44], 37 [45], 36 [47] mm ML, 1♀ submature 33 [37] mm ML, 1♀ mature 43 [54] mm ML.

Material examined found to be misidentified as P. charcoti

MNHN 5.7.1094, Admiralty Bay, King George Island, 418 m. BMNH 1919.12.30.5, 1919.12.30.29–45, *Terra Nova* Stn 338, McMurdo Sound, 379 m. BMNH 1919.12.30.18, *Terra Nova* Stn 194, off Oates Land, 329–366 m. BMNH 1919.12.30.2–4, *Terra Nova* Stn 294, Ross Sea, 289 m. BMNH 1919.12.30.17, *Terra Nova* Stn 42, off Rio de Janeiro, 73 m. BMNH 1919.12.30.1, *Terra Nova* Stn 349, McMurdo Sound, 146 m. BMNH 1951.4.26.5–17, *Discovery*, various stns, South Georgia. NMV F22851, *ANARE*, Mawson Station, 'shallow water'. NMV F65691, *ANARE*, Fram Bank, 256 m.

Comparative material examined

Moschites aurorae Berry, 1917, holotype [AM C40891], *Mawson Antarctic Expedition* stn 8, off Queen Mary Land, 66°08'S, 94°17'E, 219 m.
Pareledone framensis Lu & Stranks, 1994, paratype [NMV F65667], *RV Aurora australis* stn AA91-100, off

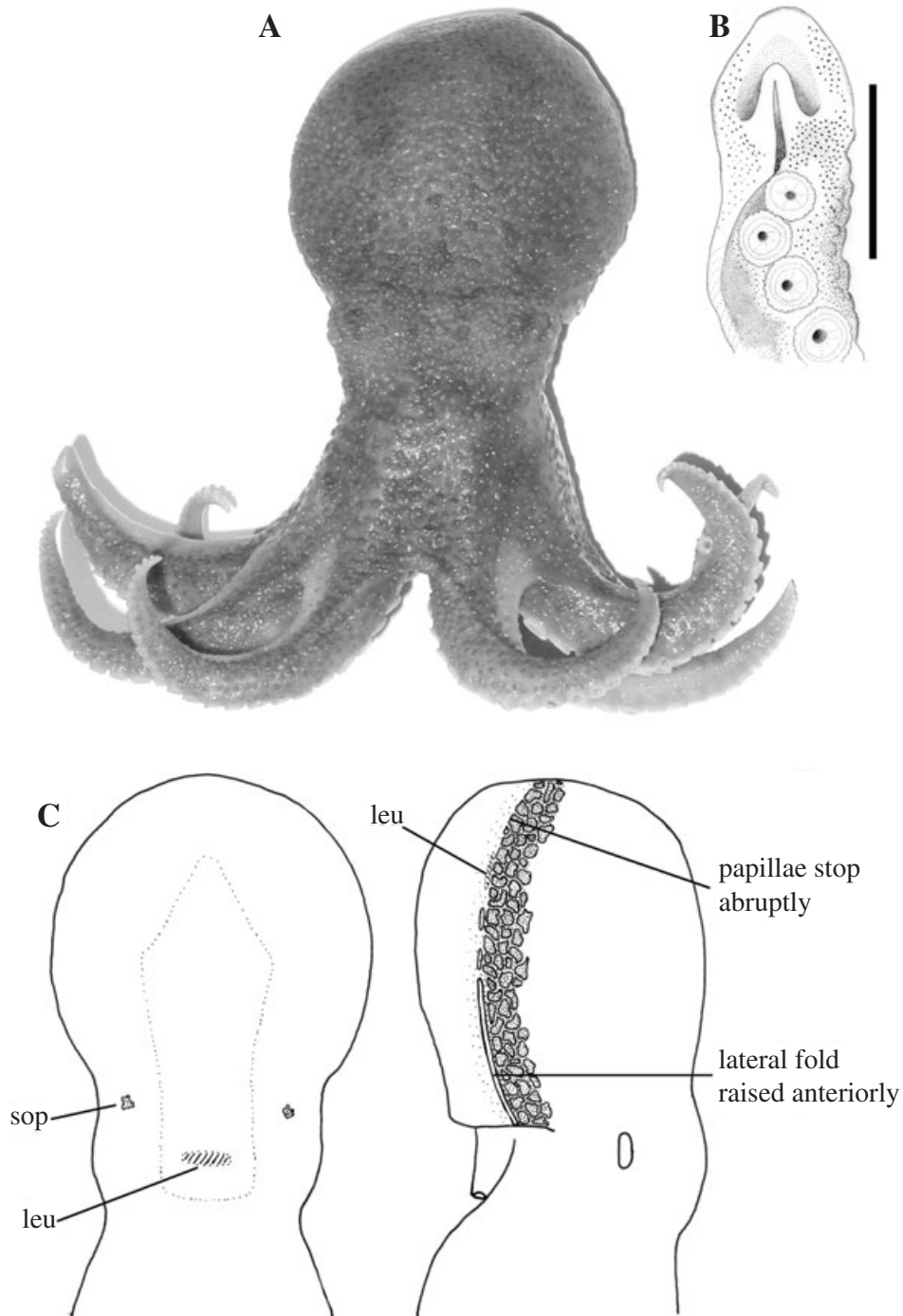


Figure 1. *Pareledone charcoti* Joubin, 1905. A, whole animal, NMSZ 2002037.044, mature ♂, 37 mm ML. B, hectocotylus, NMSZ 2002037.044, mature ♂, 37 mm ML. C, diagrammatic representation of extent of papillae and chromatophores. *Abbreviations:* leu, leucophores; sop, supraocular papillae. D, digestive system, NMSZ 2002037.044, submature ♀, 33 mm ML. E, beaks, NMSZ 2002037.044, submature ♀, 33 mm ML. F, male reproductive system, NMSZ 2002037.044, mature ♂, 36 mm ML. G, spermatophores, NMSZ 2002037.044, mature ♂, 36 mm ML. H, female reproductive system, NMSZ 2002037.044, mature ♀, 43 mm ML. I, transverse section of egg showing follicular folds. Scale bars = 5 mm.

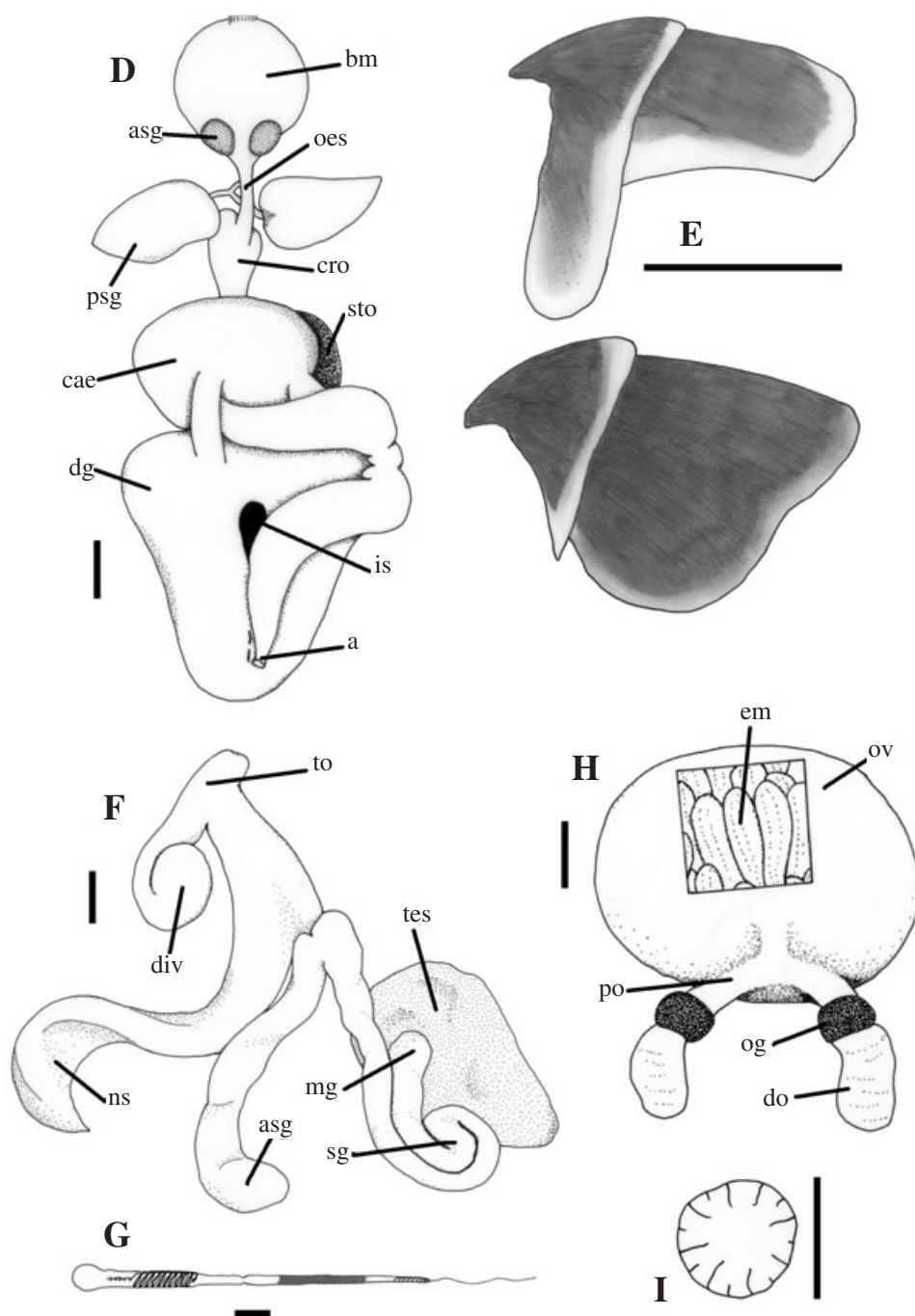


Figure 1. Continued

MacRobertson Land, 67°27.35'S, 68°50.34'E, 145–150 m.

Pareledone prydzensis Lu & Stranks, 1994, paratype [NMV F65625], *RV Aurora australis* stn AA91-89 (2), off Amery Iceshelf, 66°47'S, 72°36'W, 526–532 m.

Eledone turqueti Joubin, 1905, lectotype [MNHN 5.7.1089], 'Charcot' Antarctic Expedition, Ile Wandel, 65° 05'S, 25 m.

Moschites harrissoni Berry, 1917, holotype [AM C40892], *Mawson Antarctic Expedition* stn 10, off Shackleton Glacier, 65°06'S, 96°13'E, 494–595 m.

Moschites antarcticus Thiele, 1920; lectotype [ZMB Moll 110001a], Kaiser Wilhelm II Land, 66°47'S, 89°20'E, 385 m.

Moschites adelieana Berry, 1917, holotype [AM C40889], *Mawson Antarctic Expedition* stn 2, off Mertz Glacier, Adelieland, 66°55'S, 145°21'E, 450–549 m.

Table 1. Raw measurements from specimens of *Pareledone charcoti* used in redescription. All measurements in mm. Abbreviations: m/l, medial/lateral; l/r, left/right; d/damaged

Status	none	none	none	none	none	none	none	none	none	none	none	none	none	none	none
Repository	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ	NMSZ
Catalogue number	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044	2002037.044
Sex	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♂	♀	♂
Maturity	mature	mature	submature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature	mature
Total length	115	118	93	113	114	97	114	114	86	112	117	100			
Mantle length (dorsal)	42	36	33	37	37	36	37	37	30	36	43	35			
Mantle length (ventral)	41	33	31	35	32	30	35	35	27	29	37	27			
Mantle width	39	36	34	39	36	32	36	36	30	36	45	33			
Head width	29	26	24	26	26	25	26	26	22	27	29	25			
Pallial aperture	26	24	22	23	23	22	24	24	20	26	27	24			
Full funnel length	18	18	16	19	17	15	18	18	13	16	20	14			
Free funnel length	7	7	8	8	6	7	8	8	5	7	11	10			
Funnel organ length (m/l)	11/11	11/11	11/11	12/11	11/11	11/11	12/11	12/11	10/10	11/11	14/14	11/10			
Funnel organ shape	w	w	w	w	w	v	w	v	v	w	v	v			
Web depth sector A	18	15	16	20	16	13	13	13	14	14	17	17			
Web depth sector B (l/r)	24/21	20/19	20/22	21/20	19/20	18/18	20/20	20/20	17/17	19/19	24/22	19/18			
Web depth sector C (l/r)	28/26	21/20	23/22	23/25	25/27	22/23	24/25	24/25	18/20	24/17	27/28	21/21			
Web depth sector D (l/r)	24/26	21/21	26/22	25/24	26/26	22/22	23/23	23/23	18/19	21/22	29/28	21/21			
Web depth sector E	18	16	21	20	21	18	18	18	15	15	27	17			
Arm length L1	66	55	51	60	56	52	62	d	42	60	62	51			
Arm length L2	71	d	54	63	64	55	62	62	47	70	74	61			
Arm length L3	76	d	d	66	72	54	65	65	48	73	81	63			
Arm length Hc	64	56	60	59	67	52	59	59	45	65	80	60			
Arm length L4	75	d	60	64	70	57	63	63	47	76	80	67			
Sucker count Hc	26	28	26	26	27	26	26	26	26	27	27	27			
Sucker count L3	36	d	d	37	39	36	36	36	37	39	42	36			
Sucker diameter	4	4	4	4	3.5	3	4	4	3	4	5	3			
Arm width	7	7	6	6	7.5	6.5	6.5	6.5	5	7	8.5	5			
Ligula length	7	6	6	6	7.5	6	7.5	7.5	5.5	7.5	8.5	5			
Calamus length	3	3	3.5	3.5	4.5	3	3.5	3.5	3	3	3	2			
Gill lamellae: inner (l/r)	8/8	9/9	9/9	9/9	8/8	7/8	7/7	7/7	8/8	8/8	8/8	8/7			
Gill lamellae: outer (l/r)	7/7	8/8	8/8	8/8	8/8	7/8	7/7	7/7	8/8	8/8	7/7	8/7			
Gill length (l/r)	11/11	10/10	10/9	11/11	11/8	9/10	10/10	10/10	10/9	10/10	8/9	10/10			
Gamete length	61	51	60	55	60	57	57	57	55	55	13	55			
Gamete width	3	3	3	3	3.3	3	3	3	3	3	4	3			

Graneledone polymorpha Robson, 1930, holotype (BMNH 1951.4.26.26), *Discovery Expedition* stn 42, South Georgia, 120–204 m.

Diagnosis

Papillae are irregularly shaped and flat topped. They stop abruptly at the lateral fold. There is a single supraocular papilla over each eye. There are no other enlarged papillae. The ventral mantle is creamy white. The hectocotylized arm bears 26–28 suckers.

Redescription

Based on specimens detailed in Table 1. Animals small, ML to 43 mm, TL to 118 mm (Fig. 1A). Mantle approximately spherical (MWI 98.5 ± 5.1), head narrower than mantle (HWI 71.0 ± 2.2). Web deep (WDI 38.0 ± 4.4), web formula approximately $C = D.B.E.A$. Funnel medium-sized (FuLI 45.7 ± 3.6), gently tapered; funnel organ W- or V-shaped. Gills with 7–9 lamellae per demibranch. Arms short (MAI 56.1 ± 5.3). Arm lengths subequal, arm order usually $3 = 4.2.1$ (ALI L1151.9 ± 8.5 ; L2169.4 ± 11.3 ; L3179.0 ± 16.3 ; L4179.6 ± 16.3). Suckers uniserial, medium-sized (ASI 10.3 ± 1.2), without sucker enlargement. Third right arm of males hectocotylized, usually shorter than opposite number (OAI 90.9 ± 3.9). Ligula moderate to large (LLI 11.4 ± 0.8); ligula groove long, well-marked and shallow, without marked transverse ridges (Fig. 1B). Calamus distinct and large to very large (CaLI 50.3 ± 7.1). Hectocotylized arm with 26–28 suckers, opposite arm with up to 42 suckers. Male reproductive system (Fig. 1F) with markedly long Needham's sac storing up to 5 spermatophores. Penis large, penis diverticulum coiled. Spermatophores (Fig. 1G) long (SpLI 150.8 ± 7.2) and slender.

Female reproductive system (Fig. 1H) consists of ovary containing up to 80 eggs, paired oviducts with large dark oviducal glands. Eggs with approximately 16 follicular folds (Fig. 1I). Mature ovarian eggs large (> 10 mm). Digestive system with buccal mass approximately equal in size to posterior salivary glands (Fig. 1D). Anterior salivary glands small and closely associated with buccal mass. Short oesophagus leads into crop; crop with diverticulum. Stomach leads into coiled caecum. Anus winds around right hand side of digestive gland. Ink sac present. Anal flaps present. Beak is unremarkable (Fig. 1E), with rostral tip of lower beak rounded. Radula with nine elements, rachidian multicuspid (Fig. 10A).

Papillae are simple but irregularly shaped with a raised flat top (Fig. 9A). They cover the entire dorsal surface but stop abruptly at the lateral fold (Fig. 1C). The lateral fold is marked anteriorly (towards the pallial aperture) by a slightly raised ridge, itself sometimes marked by the presence of leucophores. Posteriorly there is no distinct division between the

dorsal and ventral mantle surfaces, except the abrupt cessation of the papillae. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle, but here they are much sparser. The centre of the ventral mantle is a creamy white colour with no evidence of chromatophores. There is an enlarged supraocular papilla. There are no other enlarged papillae on the dorsal mantle surface. A freshly dead specimen usually has a dark pink/pale brown hue. Live specimens (Fig. 11A) vary greatly in colour and may flush red when disturbed. There is often a rhomboid of paler marking on the dorsal mantle extending from between the eyes to the posterior mantle. Leucophores may be present on the head region between the eyes.

Type locality

Antarctic Peninsula. Booth-Wandel Island [$65^{\circ}05'S$, $63^{\circ}55'W$]. Shore. Expedition Antarctique Française. 3 September 1904.

Distribution

Off Graham Land [$65^{\circ}05'S$, $63^{\circ}55'W$] in rock pool (Joubin, 1905); South Shetland Islands, $60^{\circ}50'–63^{\circ}00'S$, $54^{\circ}44'–61^{\circ}49'W$, 48–392 m (this study); South Orkney Islands, $60^{\circ}43'S$, $44^{\circ}38'W$, 16–18 m (Hoyle, 1912).

Etymology

Named after Dr Charcot, leader of the Expedition Antarctique Française.

Remarks

Many of the putative specimens of *Pareledone charcoti* examined were revealed to be misidentified. In this study, 75% of specimens were found in waters shallower than 120 m (Fig. 12). Many of the misidentified specimens were from far deeper waters. Others were from outside the established range of the genus, e.g. BMNH 1919.12.30.1 from off Rio de Janeiro, or from Antarctic regions such as South Georgia where *P. charcoti* is known to be absent (see Yau *et al.*, 2002) e.g. BMNH 1951.4.26.5–17, Robson's series of *P. charcoti* which have been re-identified as *P. turqueti*.

The most significant specimen found to be misidentified is MNHN5.7.1094 referred to in Joubin's (1914) paper. Although this specimen is in poor condition it clearly has simple round papillae and cannot, under the new diagnosis of *P. charcoti*, be assigned to this species.

PARELEDONE AEQUIPAPILLAE SP. NOV.

(FIGS 2A–C, 9B, 10B, 11B; TABLE 2)

Eledone charcoti. – Joubin, 1914: 35, figs 1, 2.

Pareledone charcoti. – Piatkowski *et al.*, 1998: 43 [in part]. – Allcock, 1997: 92 [in part].

Pareledone sp. 12b. – Piatkowski *et al.* 2003.

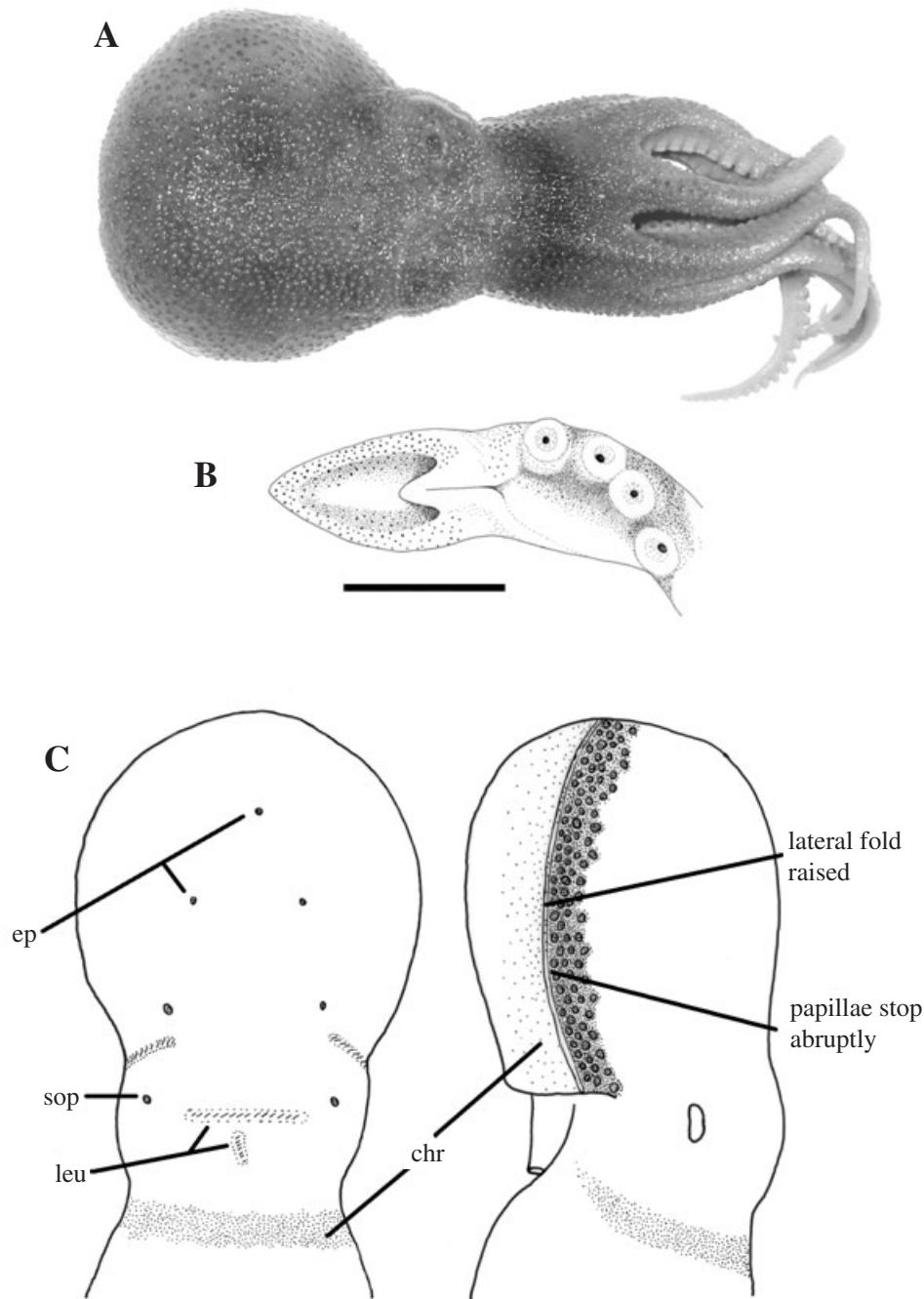


Figure 2. *Pareledone aequipapillae* sp. nov. A, whole animal, NMSZ 2002037.004, submature ♀, [34] mm ML. B, hectocotylus, NMSZ 2003152.002, mature ♂, 52 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: ep, enlarged papillae; leu, leucophores; sop, supraocular papilla.

Material examined

Holotype: NMSZ 2003152.002, *RV Polarstern*, stn 61/048–1, 30.i.2002, 61°10'S, 54°34'W, 278–343 m: 1♂ mature 52 [64] mm ML.

Paratypes: NMSZ 2002037.002, *RV Polarstern*, stn 61/048–1, 30.i.2002, 61°10'S, 54°34'W, 278–343 m: 2♀

submature 38 [48], 45 [55] mm ML, 3♀ mature 48 [61], 56 [74], 63 [78] mm ML, 4♂ mature 41 [48], 42 [48], 46 [48], 47 [58] mm ML. NMSZ 2002037.004, *RV Polarstern*, stn 61/052–1, 31.i.2002, 61°21'S, 55°14'W, 264–270 m: 2♀ immature [28], [35] mm ML, 4♀ submature [34], [44], [45], [49] mm ML, 4♂ immature [32], [34], [40], [41] mm ML.

Table 2. Raw measurements from specimens of *Pareledone aequipapillae* used in description. All measurements in mm. Abbreviations: m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype NMSZ	paratype NMSZ	holotype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ
Repository	2002037.002	2002037.002	2003152.002	2002037.002	2002037.002	2002037.002	2002037.002	2002037.002	2002037.002
Catalogue number	♀ mature	♂ mature	♂ mature	♀ submature	♂ mature	♀ mature	♂ mature	♀ submature	♂ mature
Sex	♀ mature	♂ mature	♂ mature	♀ submature	♂ mature	♀ mature	♂ mature	♀ submature	♂ mature
Maturity	♀ mature	♂ mature	♂ mature	♀ submature	♂ mature	♀ mature	♂ mature	♀ submature	♂ mature
Total length	177	157	159	141	131	191	134	117	147
Mantle length (dorsal)	56	47	52	45	42	63	41	38	46
Mantle length (ventral)	53	47	53	41	38	56	38	34	43
Mantle width	54	47	48	42	47	55	43	41	46
Head width	35	33	36	31	32	37	29	28	32
Pallial aperture	32	27	33	28	29	31	27	24	30
Full funnel length	28	23	23	23	18	27	22	20	21
Free funnel length	15	12	15	11	12	15	10	10	12
Funnel organ length (m/l)	18/18	18/18	15/14	14/14	12/13	18/18	14/14	14/14	16/16
Funnel organ shape	v	v	v	v	v	v	v	v	v
Web depth sector A	25	18	18	20	21	23	13	17	16
Web depth sector B (l/r)	27/27	18/22	21/21	21/21	21/22	23/30	18/18	19/19	17/17
Web depth sector C (l/r)	25/27	21/22	25/26	23/21	27/26	28/30	17/21	19/19	19/20
Web depth sector D (l/r)	25/27	21/23	24/24	19/17	27/22	26/28	17/21	17/17	22/20
Web depth sector E	19	18	21	12	18	20	14	11	12
Arm length L1	94	89	98	89	84	93	81	69	91
Arm length L2	94	91	103	d	80	104	80	69	91
Arm length L3	101	94	114	92	d	102	84	72	90
Arm length Hc		83	91	92	70		72		75
Arm length L4	d	96	112	92	82	104	84	73	93
Sucker count Hc		34	34		33		35		34
Sucker count L3	49	47	49	d	d	52	49	51	49
Sucker diameter	4	3.5	3	3	3	4	3	3	3
Arm width	8.5	7.5	7.5	7	7	9	6.5	7	7
Ligula length		6	9		7		6		6.5
Calamus length		3	5.5		3		2		3.5
Gill lamellae: inner (l/r)	7/7	7/7	8/7	6/7	7/7	7/7	7/7	8/8	7/7
Gill lamellae: outer (l/r)	7/8	7/7	7/8	7/7	7/7	8/7	7/7	7/8	7/7
Gill length (l/r)	13/13	17/14	13/13	13/13	13/13	15/13	12/12	14/14	11/11
Gamete length	14	92	94		82	20		16/17	93
Gamete width	7	4	4		4	9		10	4

Other material: MNHN 5.7.1094, Admiralty Bay, King George Island, 418 m

Diagnosis

Papillae are simple, round and tall. They stop abruptly at the lateral fold. There is a single supraocular papilla over each eye. There is a pattern of other enlarged papillae on the dorsal mantle. The ventral mantle is creamy white. The hectocotylized arm bears 33–35 suckers.

Description

Based on specimens detailed in Table 2. Animals small- to medium-sized, ML to 63 mm, TL to 191 mm (Fig. 2A). Mantle approximately spherical (MWI 99.4 ± 7.5), head narrower than mantle (HWI 68.4 ± 5.2). Web moderate to deep (WDI 26.0 ± 3.0), web formula approximately C = D.B.A.E. Funnel medium-sized (FuLI 48.2 ± 4.0), gently tapered; funnel organ W- or V-shaped. Gills with 6–8 lamellae per demibranch. Arms short (MAI 51.1 ± 4.2). Arm lengths subequal, arm order usually $3 = 4.1 = 2$ (ALI L1185.1 ± 16.5 ; L2185.9 ± 12.5 ; L3195.1 ± 16.4 ; L4198.2 ± 14.0). Suckers uniserial, small to medium (ASI 6.9 ± 0.6), without sucker enlargement. Third right arm of males hectocotylized, shorter than opposite number (OAI 84.3 ± 3.6). Ligula moderate to large (LLI 8.8 ± 1.2); ligula groove long, well-marked and shallow, without transverse ridges (Fig. 2B). Calamus distinct and large to very large (CaLI 48.2 ± 10.6). Hectocotylized arm with 33–35 suckers, opposite arm with up to 52 suckers. Penis diverticulum coiled. Spermatophores long to very long (SpLI 193.5 ± 9.0) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian multicupid (Fig. 10B). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae are simple and round (Fig. 9B). They are long when compared to other simple round papillae seen on *Pareledone* species and under the microscope they appear as finger-like projections. They cover the entire dorsal surface but stop abruptly at the lateral fold (Fig. 2C). Although barely raised, the lateral fold is marked by a line of leucophores. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle, but here they are much sparser. The centre of the ventral mantle is a creamy white colour with no evidence of chromatophores. There is an enlarged supraocular papilla and an indistinct pattern of slightly enlarged papillae on the dorsal mantle surface. Leucophores are often found in the head region in a characteristic pattern. An area of more dense chromatophores occurs just below the head region, forming

a band of dark colour on the dorsal surface which fades laterally and is not present ventrally. Freshly dead specimens are a grey brown colour. Live specimens (Fig. 11B) are a richer brown.

Type locality

South Shetland Islands. $61^{\circ}10'S$, $54^{\circ}34'W$, 278–343 m. *RV Polarstern*, ANT XIX/3, Stn 61/048–1, 30.i.2002.

Distribution

South Shetland Islands, $60^{\circ}49'–62^{\circ}36'S$, $55^{\circ}14'–61^{\circ}50'W$, 110–465 m (this study); King George Island, South Shetland Islands, 418 m (Joubin, 1914).

Etymology

From the Latin *aequus* (equal) and *papilla*; refers to the simple, round and even structure of the papillae.

PARELEDONE ALBIMACULATA SP. NOV.

(FIGS 3A–C, 9C, 10C, 11C; TABLE 3)

Pareledone cf. *charcoti* type 1. – Piatkowski *et al.*, 1998: 43.

Pareledone sp. 15. – Allcock, 1997: 120, pl. 4 : 16. – Piatkowski *et al.* 2003.

Material examined

Holotype: BMNH 1996192, *RV Polarstern*, stn 42/021, 21.xi.1996, $61^{\circ}19'S$, $56^{\circ}33'W$, 480 m: 1♂ mature 29 mm ML.

Paratypes: BMNH 1996193, *RV Polarstern*, stn 42/021, 21.xi.1996, $61^{\circ}19'S$, $56^{\circ}33'W$, 480 m: 1♀ mature 33 mm ML. NMSZ 2002037.007, *RV Polarstern*, stn 61/044–1, 29.i.2002, $60^{\circ}58'S$, $55^{\circ}06'W$, 308–399 m: 2♀ immature [25], [25] mm ML, 1♂ immature [18] mm ML. NMSZ 2002037.008, *RV Polarstern*, stn 61/047–1, 30.i.2002, $61^{\circ}04'S$, $54^{\circ}36'W$, 308–399 m: 2♀ mature 34 [41], 38 [46] mm ML, 1♂ immature 28 [29] mm ML, 1♂ submature 30 [35] mm ML. NMSZ 2002037.009, *RV Polarstern*, stn 61/052–1, 31.i.2002, $61^{\circ}21'S$, $55^{\circ}14'W$, 264–270 m: 1♂ mature 38 [38] mm ML. NMSZ 2002037.010, *RV Polarstern*, stn 61/101–1, 13.ii.2002, $61^{\circ}49'S$, $58^{\circ}35'W$, 321–399 m: 1♂ mature 36 [38] mm ML. NMSZ 2002037.011, *RV Polarstern*, stn 61/103–1, 13.ii.2002, $61^{\circ}45'S$, $58^{\circ}02'W$, 257–296 m: 1♀ immature 26 [26] mm ML, 2♀ submature 28 [30], 29 [34] mm ML, 1♂ mature, 31 [33] mm ML.

Diagnosis

Papillae are irregularly shaped and resemble turreted rings. They continue briefly beyond the lateral fold.

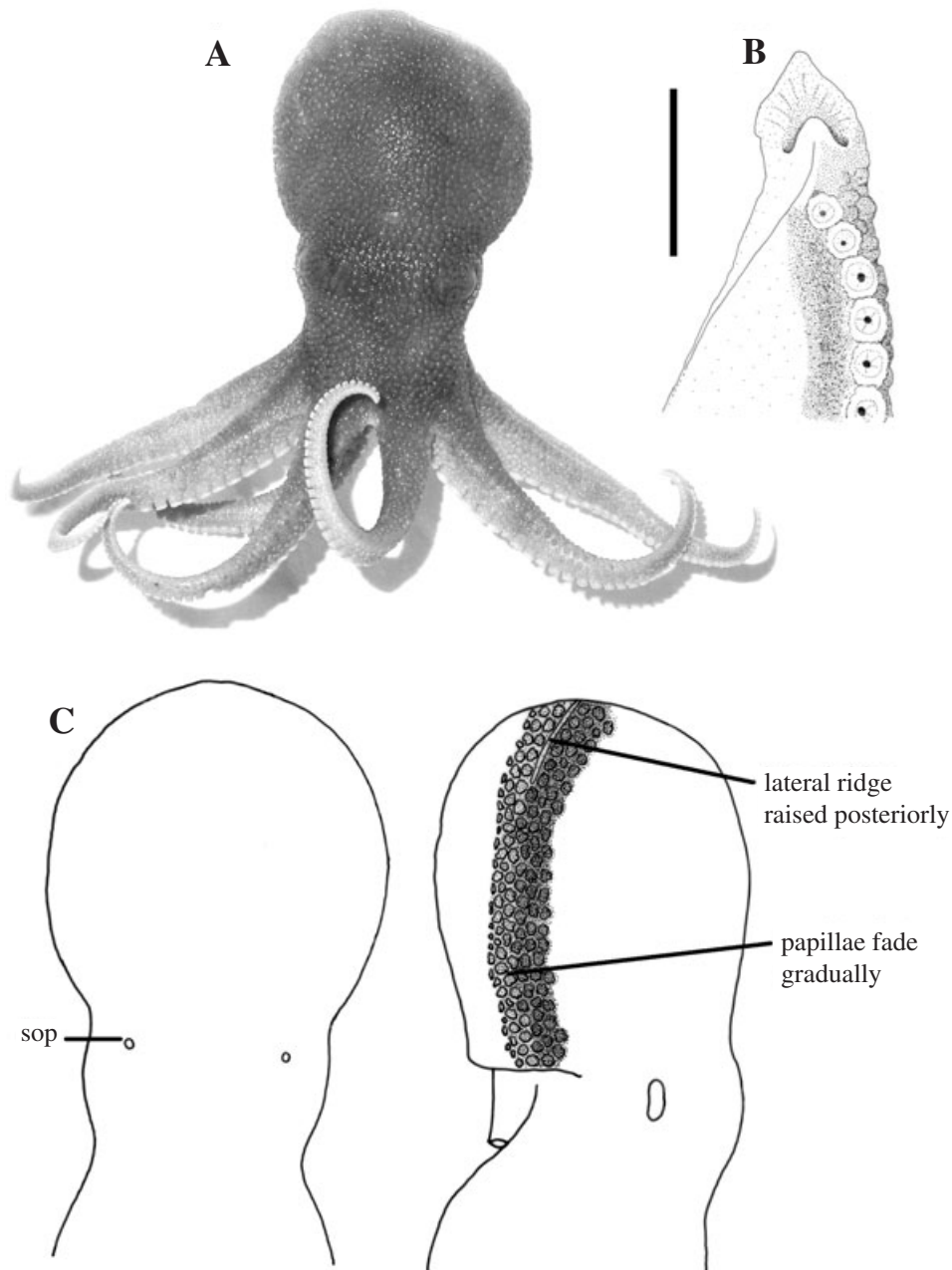


Figure 3. *Pareledone albimaculata* sp. nov. A, whole animal, NMSZ 2002037.011, submature ♀, 29 mm ML. B, hectocotylus, NMSZ 2002037.010, mature ♂, 36 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: sop, supraocular papilla.

There is a single supraocular papilla over each eye which appears as a white dot when retracted. There are no other enlarged papillae. The ventral mantle is creamy white. The hectocotylized arm bears 29–32 suckers.

Description

Based on specimens detailed in Table 3. Animals small, ML to 38 mm, TL to 133 mm (Fig. 3A). Mantle

spherical to ovoid (MWI 93.6 ± 9.5), head narrower than mantle (HWI 68.4 ± 5.8). Web moderate to deep (WDI 24.8 ± 2.8), web formula approximately $B = C = D.A = E$. Funnel medium-sized (FuLI 46.4 ± 4.0), gently tapered; funnel organ W- or V-shaped. Gills with 6–8 lamellae per demibranch. Arms short (MAI 50.1 ± 3.6). Arm lengths subequal, arm order usually $3.2.1 = 4$ (ALI L1184.4 \pm 14.7; L2192.1 \pm 10.5; L3197.6 \pm 16.6; L4184.8 \pm 17.7).

Table 3. Raw measurements from specimens of *Pareledone albimaculata* used in description. All measurements in mm. Abbreviations: m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype NMSZ 2002037.010	paratype NMSZ 2002037.011	paratype NMSZ 2002037.011	paratype NMSZ 2002037.011	paratype NMSZ 2002037.011	paratype NMSZ 2002037.008	paratype NMSZ 2002037.008	paratype NMSZ 2002037.008	paratype NMSZ 2002037.008	paratype NMSZ 2002037.008	paratype NMSZ 2002037.009	holotype BMNH 1996192
Repository Catalogue number												
Sex	♂	♀	♀	♂	♀	♀	♂	♂	♂	♂	♀	♂
Maturity	mature	submature	immature	submature	mature	mature	submature	immature	mature	mature	mature	mature
Total length	111	88	87	97	133	119	103	88	112	105		97
Mantle length (dorsal)	36	28	26	31	38	34	30	28	38	33		29
Mantle length (ventral)	31	27	24	32	34	33	28	26	37	27		21
Mantle width	32	28	25	27	41	35	29	24	28	30		26
Head width	22	19	22	21	27	24	19	17	23	24		22
Pallial aperture	18	15	16	17	24	19	16	13	18	22		19
Full funnel length	14	14	11	15	19	17	13	13	16	15		14
Free funnel length	8	7	5	7	11	10	9	7	10	8		9
Funnel organ length (m/l)	10/10	9/8	8/8	10/10	13/13	11/11	10/10	10/10	11/11	10/10		10/10
Funnel organ shape	w	v	w	w	v	v	v	w	v	v		v
Web depth sector A	14	11	10	13	17	14	10	12	15	17		136
Web depth sector B (l/r)	16/16	11/11	11/11	13/13	18/20	15/16	12/12	12/12	16/15	17/16		15/14
Web depth sector C (l/r)	16/16	11/11	11/13	14/14	15/18	15/15	15/14	12/12	17/16	20/20		16/15
Web depth sector D (l/r)	16/17	10/11	11/11	14/14	19/18	13/14	13/14	12/13	16/16	18/18		13/17
Web depth sector E	14	8	8	10	14	10	10	10	11	15		12
Arm length L1	61	51	46	51	76	70	60	50	66	58		60
Arm length L2	64	54	52	57	76	65	d	54	66	65		61
Arm length L3	67	55	52	57	83	73	d	50	67	62		65
Arm length Hc	53						49	d	59	57		52
Arm length L4	69	45	50	55	d	74	60	47	64	58		57
Sucker count Hc	29						32	d	30	31		31
Sucker count L3	41	44	45	40	50	d	d	46	46	46		49
Sucker diameter	2.5	2	2	2	3	2.5	2	2	3	2		2
Arm width	5	5	4	6	6	5	5	4	6	5		5
Ligula length	5			4			5.5		5.5			
Calamus length	2.5			1.5			2.5		2.5			
Gill lamellae: inner (l/r)	7/7	7/7	7/7	6/6	7/6	7/7	6/6	7/6	7/7	7/8		7/8
Gill lamellae: outer (l/r)	7/7	7/7	7/7	7/7	7/7	6/6/6	6/6	6/7	7/8	7/7		8
Gill length (l/r)	11/11	9/9	10/10	9/9	11/12	12/12	9/9	8/9	9/11	8/8		7/7
Gamete length	46				>1 cm				45			
Gamete width	3				-0.4 cm				2.5			

Suckers uniserial, small to medium (ASI 7.2 ± 0.7), without sucker enlargement. Third right arm of males hectocotylized, shorter than opposite number (OAI 82.4 ± 4.9). Spermatophoric groove particularly wide. Ligula moderate to large (LLI 10.0 ± 1.1); ligula groove long, well-marked and shallow, without transverse ridges but with faint radiating lines in preserved specimens (Fig. 3B). Calamus distinct and large to very large (CaLI 44.6 ± 5.2). Hectocotylized arm with 29–32 suckers, opposite arm with up to 50 suckers. Penis diverticulum coiled. Spermatophores long (SpLI 123.1 ± 6.6) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian multicuspid (Fig. 10C). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae are irregularly shaped. They are broad and both raised and slightly 'turreted' at the edges (Fig. 9C). It is not clear whether they are simple or compound; it is possible that each irregular papilla is constructed from number of small fused papillae arranged in a ring, hence the turreted appearance. They cover the entire dorsal surface and continue over the lateral fold for approximately 1 cm, decreasing in height and width away from the lateral fold (Fig. 3C). The lateral fold is marked posteriorly by a small but continuous ridge. Anteriorly (towards the pallial aperture) there is no distinct division between the dorsal and ventral mantle surfaces. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle, but here they are much sparser. They stop where the papillae cease.

The centre of the ventral mantle is a creamy white colour with no evidence of chromatophores. There is an enlarged supraocular papilla which when contracted appears as a small white spot. When extended it may be up to 5 mm in length. There are no other enlarged papillae on the dorsal mantle surface. A freshly dead specimen usually has a pink hue. Live specimens (Fig. 11C) are usually mottled pink and white.

Type locality

South Shetland Islands. $61^{\circ}19'S$, $56^{\circ}33'W$, 338–429 m. *RV Polarstern*, ANT XIV/2, Stn 42/021, 21.xi.1996.

Distribution

South Shetland Islands, $60^{\circ}50' - 62^{\circ}43'S$, $54^{\circ}37' - 58^{\circ}51'W$, 190–465 m (this study).

Etymology

From the Latin *alba* (white) and *macula* (spot); refers to the supraocular papilla which, when the animal is resting, resembles a white spot above the eye.

***PARELEDONE AURATA* SP. NOV.**

(FIGS 4A–C, 9D, 10D, 11D; TABLE 4)

Pareledone charcoti – Piatkowski *et al.*, 1998: 43 [in part]. – Allcock, 1997: 92 [in part].

Pareledone sp. 12a. – Piatkowski *et al.* 2003.

Material examined

Holotype: NMSZ 2003152.001, *RV Polarstern*, stn 61/052–1, 31.i.2002, $61^{\circ}21'S$, $55^{\circ}14'W$, 264–270 m: 1♂ mature 41 [50] mm ML.

Paratypes: NMSZ 2002037.003, *RV Polarstern*, stn 61/052–1, 31.i.2002, $61^{\circ}21'S$, $55^{\circ}14'W$, 264–270 m: 1♀ immature 26 [28] mm ML, 3♀ submature 34 [31], 42 [46], 44 [51] mm ML, 1♀ mature 49 [56] mm ML, 2♂ immature [26], 31 [37] mm ML, 3♂ submature 37 [40], 35 [42], 37 [44] mm ML.

Diagnosis

Papillae are simple and round. They mostly stop abruptly at the lateral fold except anteriorly (at the pallial aperture) where a few encroach onto the ventral surface. There is a single supraocular papilla over each eye. There are no other enlarged papillae. The ventral mantle is creamy white. The hectocotylized arm bears 27–29 suckers.

Description

Based on specimens detailed in Table 4. Animals small, ML to 49 mm, TL to 136 mm (Fig. 4A). Mantle spherical to ovoid (MWI 88.6 ± 7.3), head narrower than mantle (HWI 64.0 ± 5.5). Web deep (WDI 39.2 ± 2.7), web formula approximately C.B = D.A.E. Funnel medium-sized (FuLI 47.0 ± 3.5), gently tapered; funnel organ W- or V-shaped. Gills with 7–8 lamellae per demibranch. Arms short (MAI 65.8 ± 5.6). Arm lengths subequal, arm order usually 3 = 4.1 = 2 (ALI L1139.8 \pm 13.6; L2142.7 \pm 16.1; L3151.0 \pm 14.9; L4149.4 \pm 11.6). Suckers uniserial, small to medium (ASI 7.1 ± 0.9), without sucker enlargement. Third right arm of males hectocotylized, usually shorter than opposite number (OAI 93.6 ± 4.9). Ligula moderate to large (LLI 11.3) in only mature male examined; ligula groove long, well-marked and shallow, without transverse ridges (Fig. 4B). Calamus distinct and large (CaLI 42.9). Hectocotylized arm with 27–29 suckers, opposite arm with up to 39 suckers. Penis diverticulum coiled. Spermatophores long (SpLI 134.1) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian unicuspid (Fig. 10D). Other features of digestive and

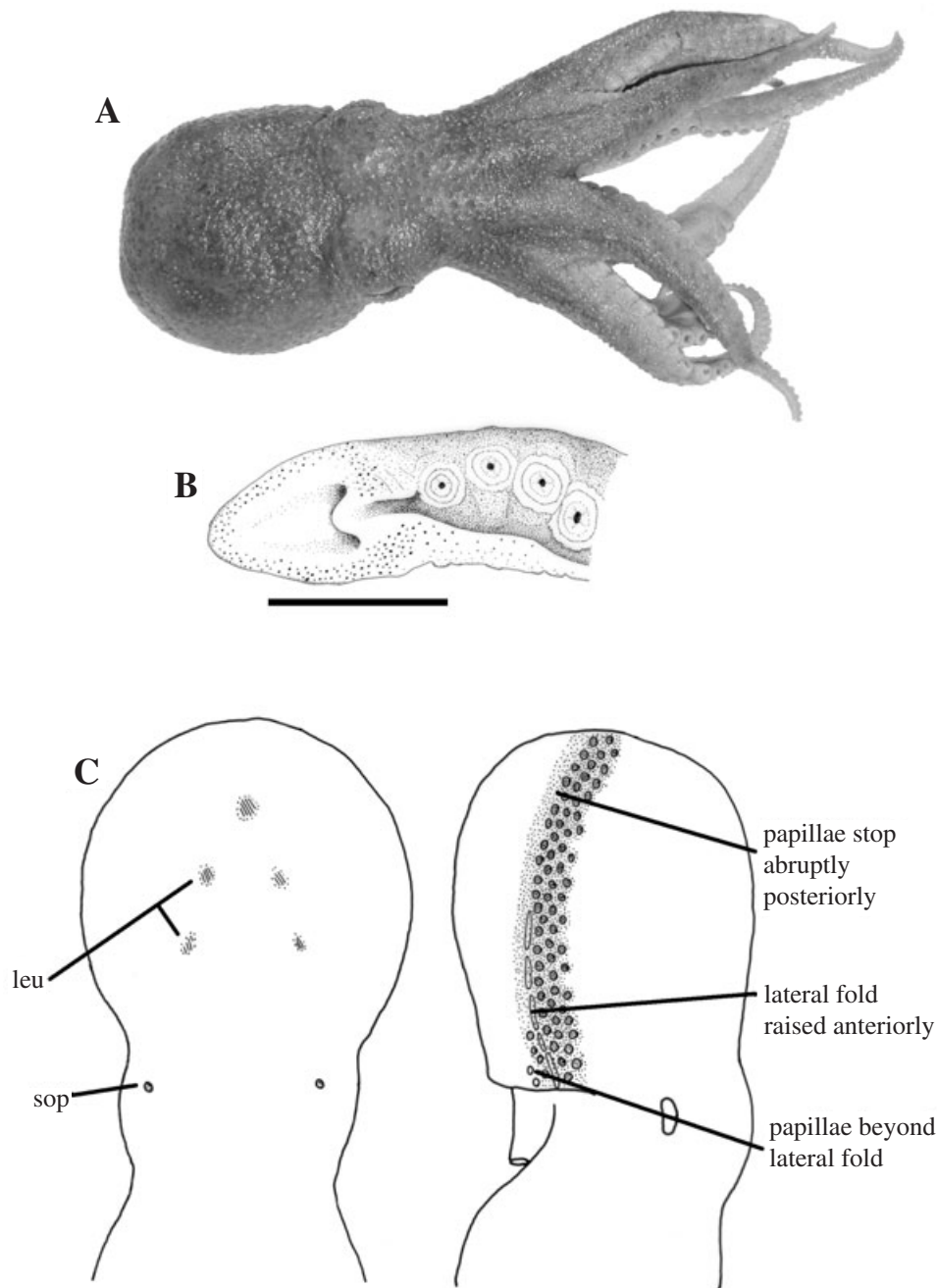


Figure 4. *Pareledone aurata* sp. nov. A, whole animal, NMSZ 2003152.001, mature ♂, 41 mm ML. B, hectocotylus, NMSZ 2003152.001, mature ♂, 41 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: leu, leucophores; sop, supraocular papilla.

reproductive systems greatly resemble those of *P. charcoti*.

Papillae are simple and round (Fig. 9D). They cover the entire dorsal surface but stop abruptly at the lateral fold, except at the anterior extreme (at the pallial aperture) where they extend a few mm on to the ventral surface (Fig. 4C). The lateral fold is marked ante-

riorly (towards the pallial aperture) by a small ridge. Posteriorly there is no distinct division between the dorsal and ventral mantle surfaces except for the abrupt cessation of papillae. Chromatophores continue a few mm beyond the lateral fold onto the surface of the ventral mantle. The centre of the ventral mantle is a creamy white colour with no evidence of

Table 4. Raw measurements from specimens of *Pareledone aurata* used in description. All measurements in mm. *Abbreviations:* m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	holotype NMSZ	paratype NMSZ
Repository	2002037.003	2002037.003	2002037.003	2002037.003	2002037.003	2002037.003	2002037.003	2003152.001	2002037.003
Catalogue number	♂	♀	♂	♀	♀	♂	♀	♂	♀
Sex	submature	submature	submature	submature	submature	submature	submature	mature	immature
Maturity	102	122	104	96	115	92	136	129	74
Total length	35	44	37	34	42	31	49	41	26
Mantle length (dorsal)	33	42	35	32	38	29	46	36	25
Mantle length (ventral)	33	39	32	31	34	25	38	37	25
Mantle width	24	26	24	22	24	20	27	30	17
Head width	21	25	20	20	22	19	25	25	17
Pallial aperture	15	22	17	15	19	16	22	12	12
Full funnel length	10	10	8	6	8	7	14	12	5
Free funnel length	12/12	13/13	11/10	11/10	13/13	10/9	14/13	14/12	9/9
Funnel organ length (m/l)	w	w	w	w	v	w	v	v	w
Funnel organ shape	19	17	18	16	15	17	23	20	13
Web depth sector A	19/19	20/21	19/23	18/19	18/19	17/18	25/20	22/22	13/14
Web depth sector B (l/r)	22/22	23/21	22/25	19/22	22/19	17/18	25/25	24/27	15/15
Web depth sector C (l/r)	19/19	22/24	17/24	20/19	22/19	17/18	23/22	24/24	15/14
Web depth sector D (l/r)	15	16	14	14	16	13	18	19	11
Web depth sector E	55	57	60	46	53	d	63	62	36
Arm length L1	55	52	61	50	53	50	66	d	35
Arm length L2	56	56	60	54	60	52	65	70	37
Arm length L3	55	62	59	51	59	46	67	62	37
Arm length Hc	27	38	37	35	34	d	36	27	29
Sucker count L3	2	3	2.5	3	3	2	3	3	2
Sucker diameter	5.5	6	4.5	5.5	5	5	6.5	7	3.5
Arm width	6.5	3	5.5	4	4	7	7	7	3
Ligula length	8/8	8/8	7/8	8/7	8/8	8/8	8/7	8/8	7/7
Calamus length (l/r)	7/7	7/7	7/7	7/7	7/7	8/8	7/7	7/7	7/7
Gill lamellae: outer (l/r)	10/11	14/14	12/11	13/13	15/15	12/11	16/16	14/12	11/9
Gill length (l/r)	34						11	55	
Gamete length	2						4.5	3	
Gamete width									

chromatophores. There is a small and indistinct (hence easily overlooked) supraocular papilla. There are no other enlarged papillae on the dorsal mantle. Leucophores are present in small irregular patches on the dorsal mantle which sometimes form a V-shape (pointing posteriorly). This patterning does not appear to be consistent. There may also be patches of leucophores on the head and brachial crown. A freshly dead specimen usually has a light blue hue. Live specimens (Fig. 11D) are usually pinker.

Type locality

South Shetland Islands. 61°21' S, 55°14' W, 264–270 m. *RV Polarstern*, ANT XIX/3, Stn 61/052–1, 31.i.2002.

Distribution

South Shetland Islands, 60°49' – 62°29'S, 55°14' – 61°25'W, 89–465 m (this study).

Etymology

From the Latin *aurata* (golden), referring to the iridophores that produce distinctive markings on the dorsal mantle and head.

***PARELEDONE CORNUTA* SP. NOV.**

(FIGS 5A–C, 9E, 10E, 11E, TABLE 5)

Pareledone cf. *charcoti* type 3. – Piatkowski *et al.*, 1998: 43

Pareledone sp. 19. – Piatkowski *et al.*, 2003. – Allcock, 1997: 130, fig. 4.9, pl. 4.18.

Material examined

Holotype: BMNH 1996196, *RV Polarstern*, stn 42/004, 16.xi.1996, 61°10' S, 56°04' W, 169–175 m: 1♂ submature 37 mm ML.

Paratypes: BMNH 1996197, *RV Polarstern*, stn 42/004, 16.xi.1996, 61°10' S, 56°04' W, 169–175 m: 1♀ submature 39 mm ML. NMSZ 2000081.041, *RV Polarstern*, stn 56/177–1, 1.v.2000, 62°50' S, 60°50' W, 200–202 m: 1♂ immature [29] mm ML, 1♂ submature [34] mm ML. NMSZ 2000081.059, *RV Polarstern*, stn 56/183–1, 3.v.2000, 62°07' S, 60°22' W, 200–204 m: 1 specimen (sex undetermined) immature [17] mm ML, 1♂ immature [22] mm ML. NMSZ 2002037.016, *RV Polarstern*, stn 61/044–1, 29.i.2002, 60°58' S, 55°06' W, 308–399 m: 1♀ immature [27] mm ML, 1♀ submature [34] mm ML, 1♀ mature 45 [49] mm ML, 1♂ mature 38 [47] mm ML. NMSZ 2002037.017, *RV Polarstern*, stn 61/045–1, 29.i.2002,

60°59' S, 55°11' W, 196–269 m: 2♀ mature 46 [56], 48 [61] mm ML, 2♂ mature [42], 43 [46] mm ML. NMSZ 2002037.018, *RV Polarstern*, stn 61/048–1, 30.i.2002, 61°10' S, 54°34' W, 278–343 m: 3♀ mature 43 [50], 47 [56], 60 [70] mm ML, 2♂ mature 38 [43], 38 [49] mm ML. NMSZ 2002037.019, *RV Polarstern*, stn 61/052–1, 31.i.2002, 61°21' S, 55°14' W, 264–270 m: 1♂ immature [32] mm ML.

Diagnosis

Papillae are large, compound and irregularly shaped. They continue briefly beyond the lateral fold. There are several supraocular papillae. There is a pattern of other enlarged papillae on the dorsal mantle. The ventral mantle is creamy white. The hectocotylyzed arm bears 29–32 suckers.

Description

Based on specimens detailed in Table 5. Animals small to medium-sized, ML to 60 mm, TL to 162 mm (Fig. 5A). Mantle approximately spherical (MWI 98.1 ± 5.5), head narrower than mantle (HWI 69.1 ± 5.1). Web deep (WDI 31.0 ± 2.6), web formula approximately $C = D.B = E.A$. Funnel medium-sized (FuLI 43.3 ± 4.7), gently tapered; funnel organ W- or V-shaped. Gills with 7–9 lamellae per demibranch. Arms short (MAI 57.5 ± 3.7). Arm lengths subequal, arm order usually $3 = 4.2.1$ (ALI $L1147.6 \pm 12.2$; $L2157.5 \pm 12.5$; $L3168.2 \pm 13.1$; $L4172.6 \pm 10.0$). Suckers uniserial, small to medium (ASI 7.3 ± 0.8), without sucker enlargement. Third right arm of males hectocotylyzed, shorter than opposite number (OAI 87.6 ± 2.9). Ligula moderate to large (LLI 9.3 ± 0.8); ligula groove long, well-marked and shallow, with faint transverse ridges (Fig. 5B). Calamus distinct and moderate to large (CaLI 34.1 ± 8.7). Hectocotylyzed arm with 29–32 suckers, opposite arm with up to 49 suckers. Penis diverticulum coiled. Spermatophores long (SpLI 168.9 ± 18.1) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian multicuspoid (Fig. 10E). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae are very large, compound (with extensive branching) and irregularly shaped (Fig. 9E). They cover the entire dorsal surface and continue over the lateral fold for approximately 1 cm, decreasing in height and width away from the lateral fold (Fig. 5C). The lateral fold is marked posteriorly where papillae are positioned in a close set line and may be slightly extended, sometimes with leucophores at the extremes. Anteriorly (towards the pallial aperture) there is no distinct division between the dorsal and

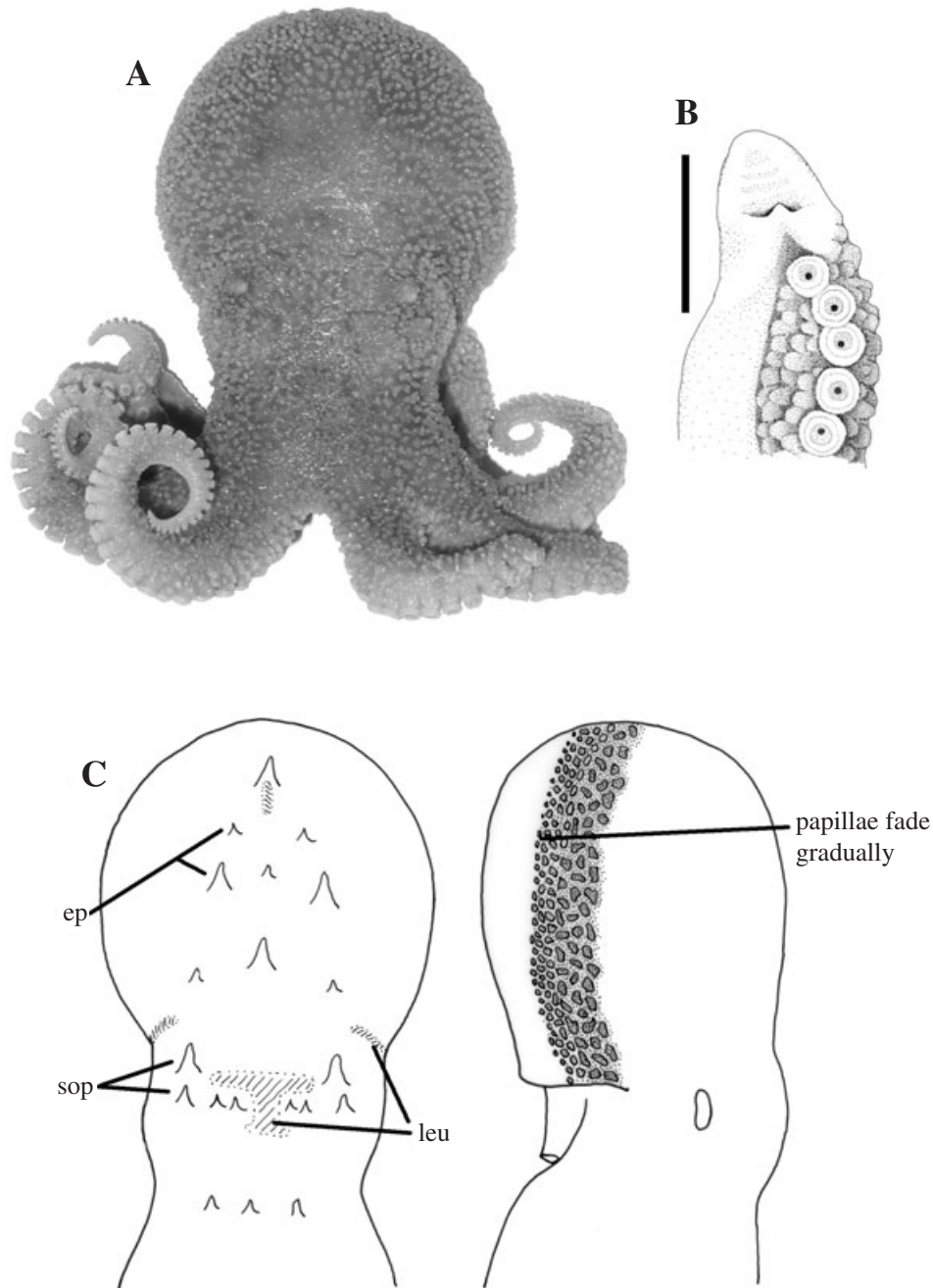


Figure 5. *Pareledone cornuta* sp. nov. A, whole animal, NMSZ 2002037.018, mature ♀, 47 mm ML. B, hectocotylus, NMSZ 2002037.018, mature ♂, 38 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: ep, enlarged papillae; leu, leucophores; sop, supraocular papilla.

ventral mantle surfaces, although there may be some leucophores in this region. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle, but here they are much sparser. They stop where the papillae cease. The centre of the ventral mantle is a creamy white colour with no evidence of chromatophores. There are multiple supraocular papillae, two of which are particularly enlarged. The

largest may extend to 10 mm in length. There is a distinctive pattern of enlarged papillae on the dorsal mantle surface and a distinctive pattern of leucophores, although the latter does display a degree of variability. A freshly dead specimen usually has a light brown hue. Live specimens (Fig. 11E) are usually darker and redder; they can use their papillae to alter their external appearance.

Table 5. Raw measurements from specimens of *Pareledone cornuta* used in description. All measurements in mm. Abbreviations: m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype NMSZ 2002037.018	♂ mature	paratype NMSZ 2002037.018	♀ mature	paratype NMSZ 2002037.018	♀ mature	paratype NMSZ 2002037.018	♂ mature	paratype NMSZ 2002037.017	♀ mature	paratype NMSZ 2002037.017	♀ mature	paratype NMSZ 2002037.016	♂ mature	paratype NMSZ 2002037.016	♀ submature	holotype BMNH 1996196
Total length	112	113	127	125	162	162	121	138	138	134	121	120	121	120	120	90	
Mantle length (dorsal)	38	38	43	47	60	60	43	46	48	45	38	39	38	38	39	37	
Mantle length (ventral)	36	37	36	43	57	57	32	42	42	45	35	31	35	31	31	30	
Mantle width	38	37	41	47	56	56	44	43	47	43	42	40	42	40	40	33	
Head width	28	27	30	33	36	36	28	31	32	29	30	29	30	29	29	25	
Pallial aperture	21	22	26	29	29	29	24	27	28	27	28	23	27	23	23	22	
Full funnel length	17	16	21	23	28	28	16	22	21	21	14	15	14	15	14	14	
Free funnel length	9	10	9	11	17	17	9	10	9	12	7	8	7	8	7	7	
Funnel organ length (m/l)	10/8	12/12	12/12	12/12	18/18	18/18	12/12	16/15	14/12	12/10	8/8	10/10	8/8	10/10	10/10	9/8	
Funnel organ shape	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	w	
Web depth sector A	13	18	15	19	21	21	14	20	21	21	14	18	14	18	13	13	
Web depth sector B (l/r)	15/16	19/20	16/19	20/21	23/23	23/23	16/19	23/25	22/22	22/24	16/17	19/19	16/17	19/19	14/15	14/15	
Web depth sector C (l/r)	20/20	21/21	22/21	24/25	27/28	27/28	20/19	27/30	25/24	23/24	21/21	20/20	21/21	20/20	16/16	16/16	
Web depth sector D (l/r)	17/20	22/22	22/23	24/25	29/29	29/29	19/18	27/32	25/24	23/25	21/21	22/22	21/21	22/22	18/17	18/17	
Web depth sector E	16	21	18	18	25	25	17	22	19	20	15	21	15	21	14	14	
Arm length L1	55	63	d	65	84	84	55	72	72	68	62	60	62	60	49	49	
Arm length L2	57	67	67	66	d	d	67	71	78	69	68	64	68	64	52	52	
Arm length L3	61	67	72	73	93	93	74	87	82	73	71	69	71	69	54	54	
Arm length Hc	53	60					62				64				47	47	
Arm length L4	65	70	76	73	96	96	72	85	85	76	66	73	66	73	30	30	
Sucker count Hc	29	32	39	47	44	44	46	49	43	47	47	46	47	46	45	45	
Sucker count L3	44	47	3	4	4.5	4.5	3	3.5	3.5	3.5	3	3	3	3	2	2	
Sucker diameter	2.5	6.5	7.5	8	10	10	8	8	7.5	7.5	5.5	8	5.5	8	7	7	
Arm width	6	6.5					5.5				5.5		5.5				
Ligula length	5.5	5.5					2.5				1.5		1.5				
Calamus length	2	1.5					2.5				1.5		1.5				
Gill lamellae: inner (l/r)	8/8	7/7	7/7	7/7	7/7	7/7	9/9	8/8	8/8	7/8	7/7	7/7	7/7	7/7	7/7	8/8	
Gill lamellae: outer (l/r)	8/8	7/7	8/8	7/7	8/7	8/7	8/8	8/7	7/8	7/7	7/7	7/7	7/7	7/7	7/7	7/8	
Gill length (l/r)	11/11	14/14	11/12	12/12	11/11	11/11	12/13	13/14	14/13	16/16	10/10	11/11	10/10	11/11	10/10	10/10	
Gamete length	64	67	14	14	20	20	32	12	14	10	71	10	71	10	71	71	
Gamete width	3	3	5	6	9	9	3	5	6	5	3	5	3	5	3	3	

Type locality

South Shetland Islands. 61°10'S, 56°04'W. 169–175 m.
RV Polarstern, ANT XIV/2, Stn 42/004, 16.xi.1996.

Distribution

South Shetland Islands, 60°49'–62°50'S, 54°34'–60°49'W, 130–454 m (this study).

Etymology

From the Latin *cornuta* (horned), referring to the very large supraocular papillae found in this species.

***PARELEDONE PANCHROMA* SP. NOV.**

(FIGS 6A–C, 9F, 10F, 11F; TABLE 6)

Graneledone sp. – Piatkowski *et al.*, 1998: 43
 ?*Graneledone* sp. 29. – Allcock, 1997: 85, fig. 4.2.
 sp. 29. – Piatkowski *et al.* 2003.

Material examined

Holotype: NMSZ 2003152.005, *RV Polarstern*, stn 56/178–2, 2.v.2000, 61°59'S, 60°19'W, 804–930 m: 1♂ mature 33 [44] mm ML.

Paratypes: NMSZ 2000081.051, *RV Polarstern*, stn 56/178–2, 2.v.2000, 61°59'S, 60°19'W, 804–930 m: 2♀ immature [33], [34] mm ML, 1♀ submature 29 [43] mm ML, 2♀ mature 43 [48], 41 [50] mm ML, 4♂ mature 28 [35], 32 [38], 34 [40], 35 [40] mm ML. NMSZ 2000081.060, *RV Polarstern*, stn 56/178–2, 2.v.2000, 61°59'S, 60°19'W, 804–930 m: 1♀ submature 32 [39] mm ML. NMSZ 2002037.023, *RV Polarstern*, stn 61/098–1, 10.ii.2002, 61°06'S, 56°07'W, 442–458 m: 2♂ mature [28], [31] mm ML. NMSZ 2002037.024, *RV Polarstern*, stn 61/101–1, 13.ii.2002, 61°49'S, 58°35'W, 321–399 m: 1♂ submature [26] mm ML. NMSZ 2002037.025, *RV Polarstern*, stn 61/120–1, 18.ii.2002, 62°11'S, 60°48'W, 413–472 m: 1♀ mature 36 [39] mm ML.

Diagnosis

Papillae are irregularly shaped, stopping abruptly at the lateral fold. There are no enlarged papillae of any kind. The ventral mantle is densely covered in chromatophores. The hectocotylized arm bears 23–25 suckers. Ink sac and anal flaps are absent.

Description

Based on specimens detailed in Table 6. Animals small, ML to 43 mm, TL to 105 mm (Fig. 6A). Mantle spherical to ovoid (MWI 94.5 ± 7.8), head narrower than mantle (HWI 71.3 ± 8.0). Web deep (WDI 41.1 ± 5.6), web formula approximately B = C =

D.A = E. Funnel medium-sized (FuLI 47.2 ± 5.5), gently tapered; funnel organ W- or V-shaped. Gills with 6–8 lamellae per demibranch. Arms short (MAI 73.4 ± 6.4). Arm lengths subequal, arm order usually 2 = 3 = 4.1 (ALI L1123.7 ± 8.6; L2128.9 ± 5.8; L3128.6 ± 10.0; L4131.8 ± 11.7). Suckers uniserial, small to medium (ASI 6.6 ± 0.9), without sucker enlargement. Third right arm of males hectocotylized, approximately equal to or longer than opposite number (OAI 105.2 ± 5.2). Ligula moderate to large (LLI 10.4 ± 1.4); ligula groove long, well-marked and shallow, without transverse ridges (Fig. 6B). Calamus distinct and large to very large (CaLI 49.2 ± 7.1). Hectocotylized arm with 23–25 suckers, opposite arm with up to 36 suckers. Penis diverticulum coiled. Spermatophores medium to long (SpLI 118.6 ± 15.3) and slender. Mature ovarian eggs large (> 10 mm). Ink sac absent. Anal flaps absent. Radula with nine elements, rachidian multicuspid (Fig. 10F). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae are compound, although they are not as large and elaborate as those of *P. cornuta* and their structure may be hard to discern in fixed material (Fig. 9F). They cover the entire dorsal surface but stop abruptly at the lateral fold (Fig. 6C). The lateral fold is unmarked; there is no distinct division between the dorsal and ventral mantle surfaces, except the abrupt cessation of the papillae. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle. They cover the entire ventral surface at a density similar to that found on the dorsal surface. There are no enlarged papillae on the dorsal mantle surface. Leucophores may be present as a bar between the eyes and as other patches on the anterior dorsal mantle. Freshly dead and live specimens (Fig. 11F) both have a deep purple hue.

Type locality

South Shetland Islands. 61°59'S, 60°19'W. 804–930 m.
RV Polarstern, ANT XVII/3, Stn 56/178–2, 02.v.2000.

Distribution

South Shetland Islands, 61°06'–62°19'S, 56°07'–60°48'W, 427–804 m (this study).

Etymology

From the Greek *pan* (everywhere) and *chromus* (colour); refers to the intense coloration that covers the entire animal.

Remarks

This species lacks an ink sac and under the traditional scheme proposed by Voss (1988) would be placed in the *Graneledone*. However, it is now widely recognized

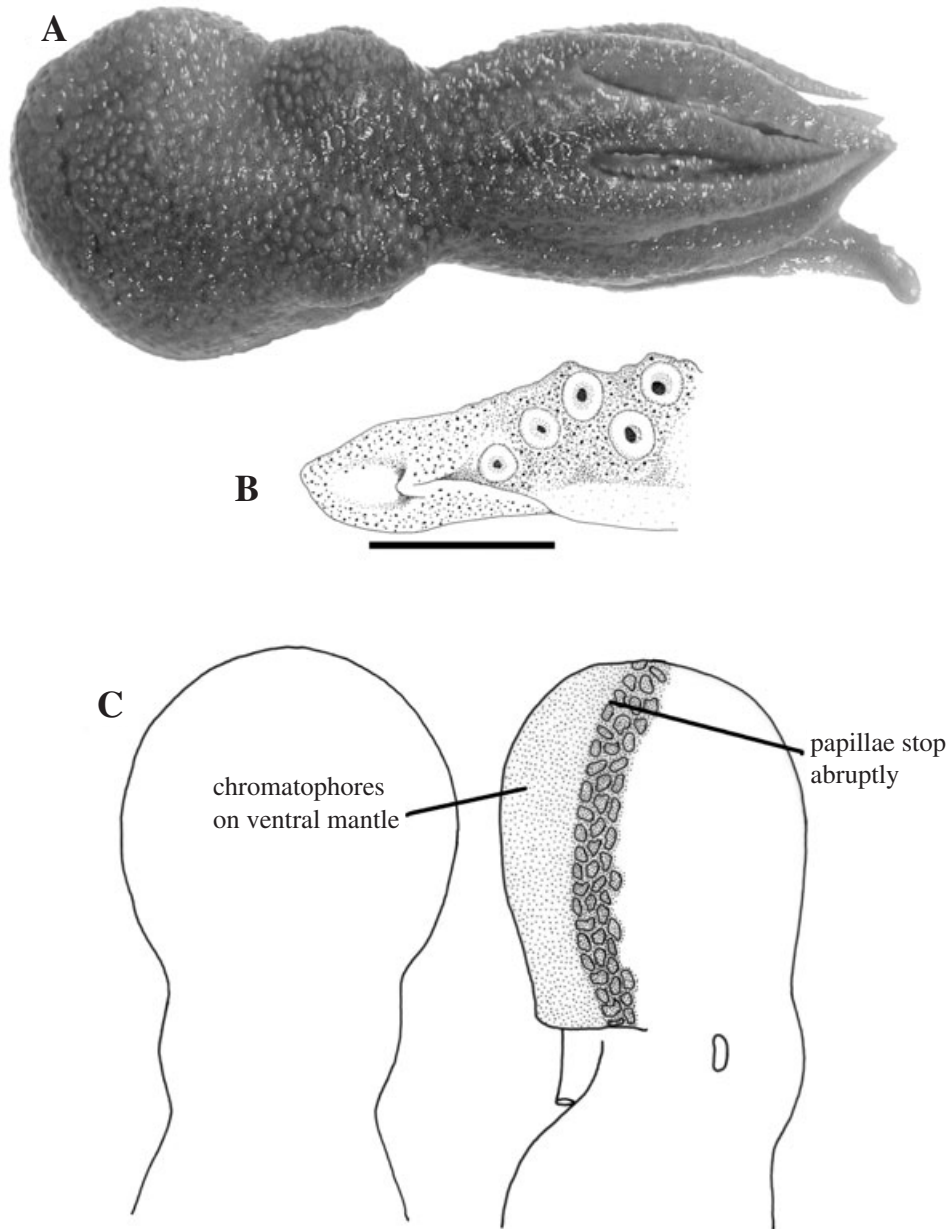


Figure 6. *Pareledone panchroma* sp. nov. A, whole animal, NMSZ 2002037.023, mature ♂, [28] mm ML. B, hectocotylus, NMSZ 2003152.005, mature ♂, 33 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores.

that lack of an ink sac is a degenerate character associated with increasing depth (e.g. Allcock *et al.*, 2003) and the other characteristics described above clearly indicate that this species belongs in *Pareledone*.

***PARELEDONE SERPERASTRATA* SP. NOV.**

(FIGS 7A–C, 9G, 10G, 11G, TABLE 7)

Pareledone sp. 2. – Piatkowski *et al.*, 1998: 43

Pareledone sp. 26. – Piatkowski *et al.* 2003. – Allcock, 1997: 810, pl. 4.1.

Material examined

Holotype: NMSZ 2003152.003, *RV Polarstern*, stn 61/092–1, 9.ii.2002, 61°01'S, 55°46'W, 123–159 m: 1♂ mature 36 [38] mm ML.

Paratypes: NMSZ 2002037.020, *RV Polarstern*, stn 61/045–1, 29.i.2002, 60°59'S, 55°11'W, 196–269 m: 1♀ submature 33 [38] mm ML. NMSZ 2002037.021, *RV Polarstern*, stn 61/092–1, 9.ii.2002, 61°01'S, 55°46'W, 123–159 m: 2♀ submature 29 [30], 32 [32]

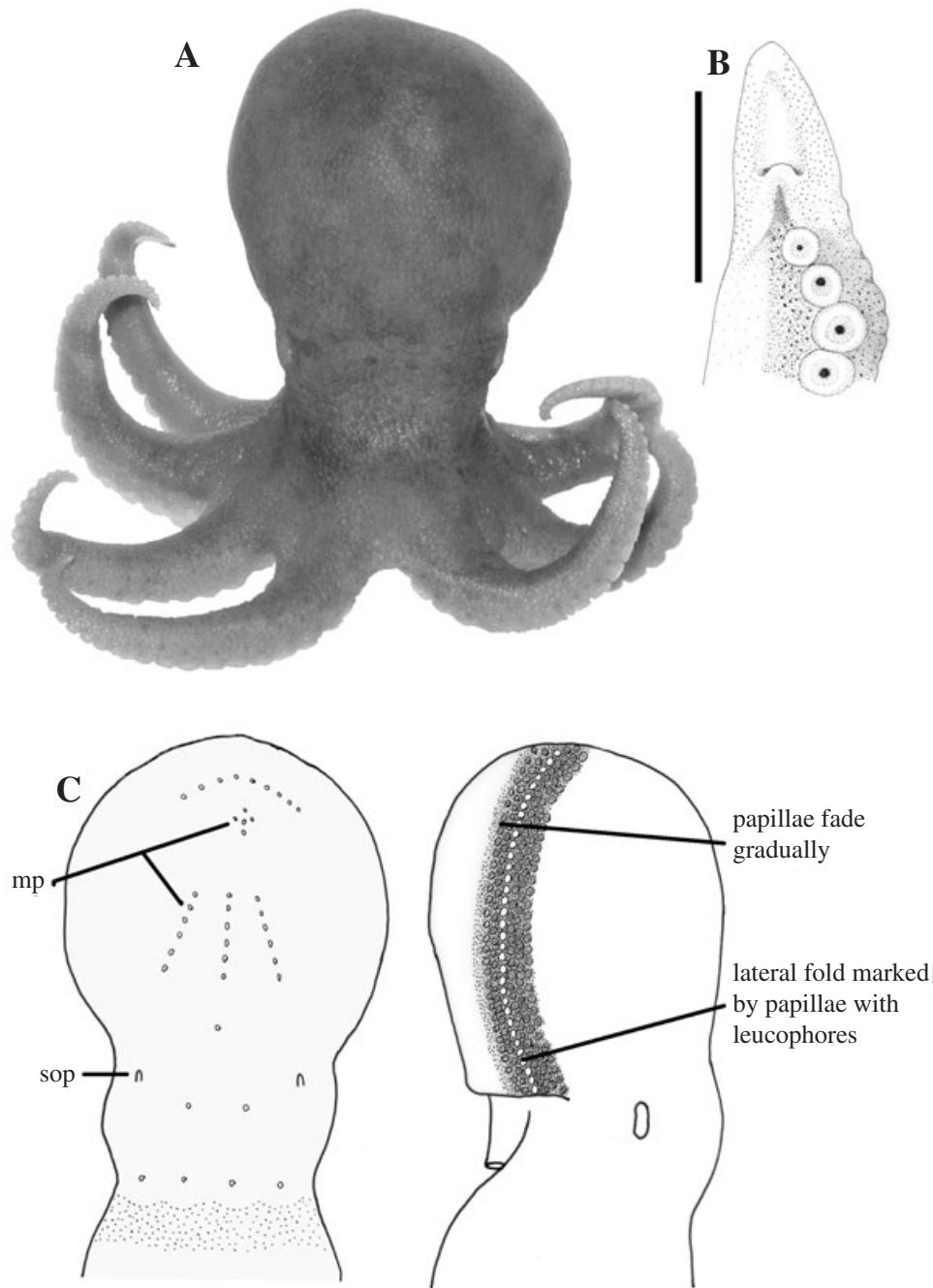


Figure 7. *Pareledone serperastrata* sp. nov. A, whole animal, NMSZ 2002037.021, submature ♀, 29 mm ML. B, hectocotylus, NMSZ 2003152.003, mature ♂, 36 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: mp, modified papillae; sop, supraocular papilla.

mm ML. NMSZ 2002037.022, *RV Polarstern*, stn 61/093–1, 9.ii.2002, 61°01'S, 55°46'W, 153–184 m: 1♀ immature 21 [21] mm ML, 2♀ submature 23 [25], 30 [31] mm ML. NMSZ 2002037.047, *RV Polarstern*, stn 61/101–1, 13.ii.2002, 61°49'S, 58°35'W, 321–399 m: 1 specimen (sex undetermined) immature [11] mm ML.

Diagnosis

Papillae are round and very small. They continue briefly beyond the lateral fold. There is a single supraocular papilla over each eye, and a pattern of modified papillae on the dorsal mantle. The ventral mantle is creamy white. The hectocotylized arm bears approximately 26 suckers.

Table 7. Raw measurements from specimens of *Pareledone serperastrata* used in description. All measurements in mm. Abbreviations: m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	holotype NMSZ	paratype NMSZ	paratype NMSZ	paratype NMSZ	none
Repository	2002037.020	2002037.022	2002037.022	2002037.022	2003152.003	2002037.021	2002037.021	2002037.021	BMNH
Catalogue number	♀	♀	♀	♀	♂	♀	♀	♀	none
Sex	submature	submature	submature	immature	mature	submature	submature	submature	♂
Maturity									submature
Total length	92	84	69	59	104	88	86	86	
Mantle length (dorsal)	33	30	23	21	36	32	29	29	32
Mantle length (ventral)	32	31	22	19	34	30	29	29	26
Mantle width	32	30	25	20	34	30	30	30	28
Head width	23	21	17	19	24	21	20	20	22
Pallial aperture	20	17	14	14	19	18	17	17	19
Full funnel length	14	13	10	9	14	16	15	15	12
Free funnel length	8	8	5	5	8	9	7	7	8
Funnel organ length (m/l)	10/10	9/8	7/7	7/7	9/9	10/9	11/9	11/9	10/10
Funnel organ shape	w	w	w	v	w	w	w	w	v
Web depth sector A	13	13	11	10	17	15	14	14	15
Web depth sector B (l/r)	14/15	16/14	13/13	11/10	18/17	17/17	16/15	16/15	15/15
Web depth sector C (l/r)	16/16	17/16	15/13	12/10	21/19	19/18	16/17	16/17	16/15
Web depth sector D (l/r)	16/16	17/16	13/13	12/10	20/20	18/17	14/17	14/17	16/17
Web depth sector E	13	14	9	8	9	13	11	11	12
Arm length L1	50	43	37	30	62	40	44	44	55
Arm length L2	d	45	40	32	58	d	d	d	54
Arm length L3	47	45	41	34	62	45	47	47	d
Arm length Hc					59				51
Arm length L4	49	48	40	32	62	45	d	d	55
Sucker count Hc					26				24
Sucker count L3	30	26	29	27	32	25	31	31	
Sucker diameter	3.5	3	2	1.5	3	3	3	3	2
Arm width	6	6	4.5	4	6.5	5.5	6	6	5
Ligula length					5				
Calamus length	7/7	8/7	7/7	7/7	1.5	7/7	7/7	7/7	7/7
Gill lamellae: inner (l/r)	7/7	7/7	7/7	7/7	7/7	8/7	7/7	7/7	7/7
Gill lamellae: outer (l/r)	12/12	10/10	7/7	6/6	12/12	11/10	9/10	9/10	6/6
Gill length (l/r)	7				52	7			9/8
Gamete length	3				2.5	2			
Gamete width									

Description

Based on specimens detailed in Table 7. Animals small, ML to 36 mm, TL to 104 mm (Fig. 7A). Mantle approximately spherical (MWI 98.9 ± 5.5), head narrower than mantle (HWI 72.2 ± 8.5). Web deep (WDI 35.9 ± 3.2), web formula approximately $B = C = D.A = E$. Funnel medium-sized (FuLI 44.7 ± 4.5), gently tapered; funnel organ W- or V-shaped. Gills with 6–8 lamellae per demibranch. Arms short (MAI 62.5 ± 5.0). Arm lengths subequal, arm order usually $2 = 3 = 4.1$ (ALI L1149.6 \pm 14.9; L2159.4 \pm 10.8; L3158.2 \pm 14.4; L4157.9 \pm 13.3). Suckers uniserial, medium-sized (ASI 9.2 ± 1.2), without sucker enlargement. Third right arm of males hectocotylized, shorter than opposite number (OAI 95.2) in only mature male examined. Ligula moderate to large (LLI 8.5); ligula groove long, well-marked and shallow, without transverse ridges (Fig. 7B). Calamus distinct and moderate to large (CaLI 30.0). Hectocotylized arm with 26 suckers, opposite arm with up to 32 suckers. Penis diverticulum coiled. Spermatophores long (SpLI 144.4) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian multicuspid (Fig. 10G). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae are simple, round and extremely small (Fig. 9G). They cover the entire dorsal surface and continue over the lateral fold for a few millimetres (Fig. 7C). The lateral fold is marked by a close set line of papillae that apparently contain leucophores. The line extends both posteriorly and anteriorly. Chromatophores continue beyond the lateral fold onto the surface of the ventral mantle; they extend slightly further than the papillae. There is an enlarged supraocular papilla. There are other papillae that stand out, but this is due to the presence of leucophores in their tips rather than enlargement. These distinct papillae usually show a characteristic pattern. There are also small round patches of leucophores spaced regularly half-way down each arm, giving the animal the appearance of wearing knee bandages. In preserved specimens these areas appear pink. A band of denser chromatophores is found just below the head. A freshly dead specimen usually has a grey hue. Live specimens (Fig. 11G) are usually pinker.

Type locality

South Shetland Islands. 61°01'S, 55°46'W. 123–159 m. *RV Polarstern*, ANT XIX/3, Stn 61/092–1, 09.ii.2002.

Distribution

South Shetland Islands, 60°49'–62°50'S, 54°34'–60°49'W, 130–454 m (this study).

Etymology

From the Latin *serperastrum* (bandages, knee-splints), referring to the regular arrangement of white patches on the arms of this species.

***PARELEDONE SUBTILIS* SP. NOV.**

(FIGS 8A–C, 9H, 10H, 11H; TABLE 8)

Pareledone sp. 33. – Piatkowski *et al.* 2003.

Material examined

Holotype: NMSZ 2003152.004, *RV Polarstern*, stn 61/047–1, 30.i.2002, 61°04'S, 54°36'W, 308–399 m: 1♂ mature 34 [36] mm ML.

Paratypes: NMSZ 2002037.026, *RV Polarstern*, stn 61/047–1, 30.i.2002, 61°04'S, 54°36'W, 308–399 m: 1♀ immature [21] mm ML, 4♀ submature [28], [31], [34], [34] mm ML, 4♀ mature 36 [41], 35 [43], 39 [45], 43 [52] mm ML, 1♂ mature 27 [30] mm ML. NMSZ 2002037.027, *RV Polarstern*, stn 61/103–1, 13.ii.2002, 61°45'S, 58°02'W, 257–296 m: 2♀ mature 39 [43], 44 [51] mm ML, 1♂ mature 31 [36] mm ML.

Diagnosis

Papillae appear simple and round to naked eye, but less regular under microscope. They stop abruptly at the lateral fold. There are no enlarged papillae of any kind. The ventral mantle is covered in chromatophores although these are less dense than on the dorsal surface. The hectocotylized arm bears approximately 24 suckers.

Description

Based on specimens detailed in Table 8. Animals small, ML to 44 mm, TL to 109 mm (Fig. 8A). Mantle spherical to ovoid (MWI 91.2 ± 5.8), head narrower than mantle (HWI 62.1 ± 6.2). Web deep (WDI 40.2 ± 2.6), web formula approximately $B = C = D.A.E$. Funnel medium-sized (FuLI 45.8 ± 5.7), gently tapered; funnel organ W- or V-shaped. Gills with 6–8 lamellae per demibranch. Arms short (MAI 70.1 ± 6.5). Arm lengths approximately equal (ALI L1137.7 \pm 12.6; L2143.0 \pm 10.8; L3140.4 \pm 12.1; L4139.9 \pm 16.6). Suckers uniserial, small to medium (ASI 6.9 ± 0.8), without sucker enlargement. Third right arm of males hectocotylized, usually shorter than opposite number (OAI 94.5 ± 2.6). Ligula moderate to large (LLI 10.0 ± 1.6); ligula groove long, well-marked and shallow, without transverse ridges (Fig. 8B). Calamus distinct and large to very large (CaLI 53.7 ± 3.2). Hectocotylized arm with approximately 24 suckers, opposite arm

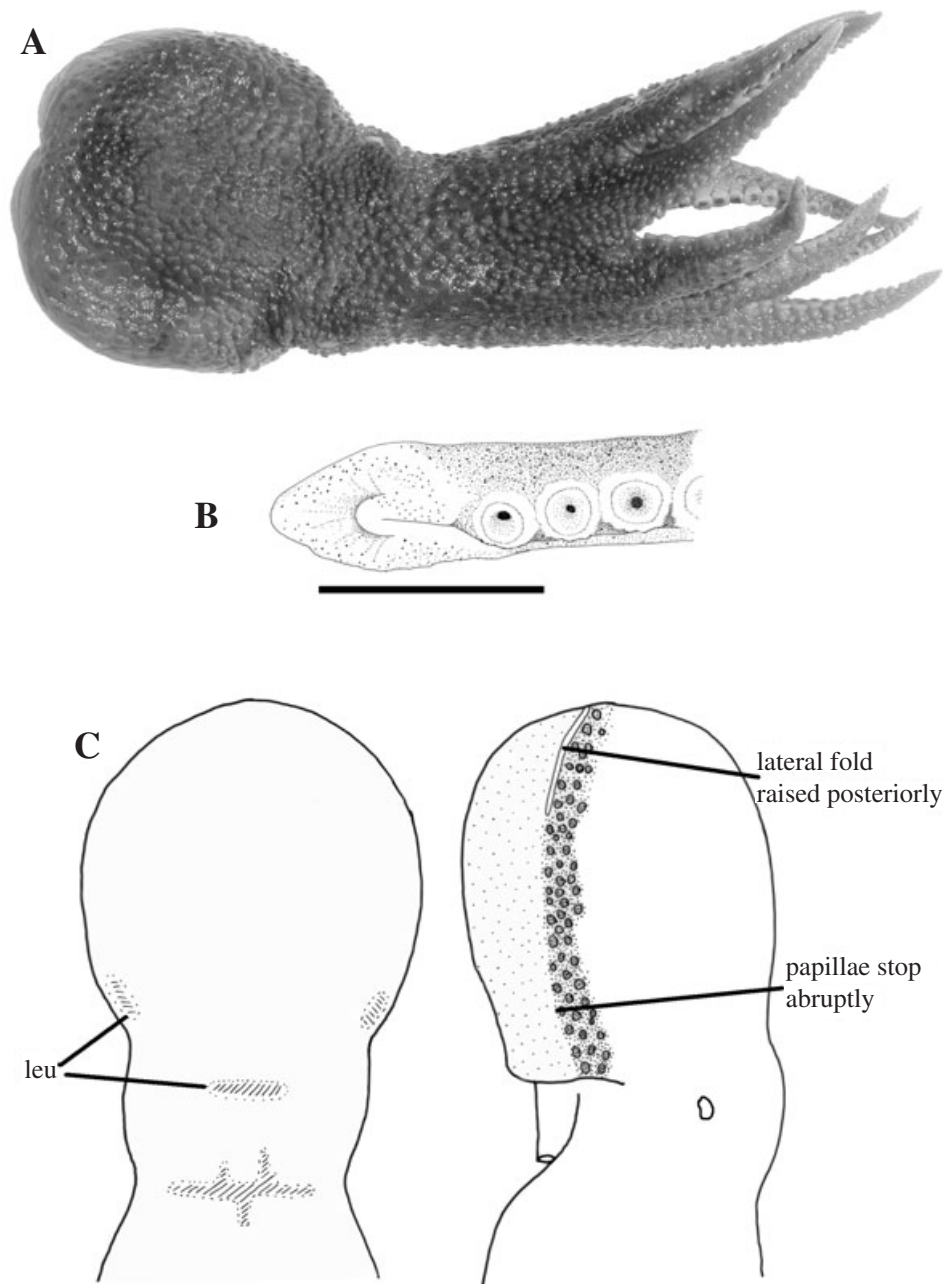


Figure 8. *Pareledone subtilis* sp. nov. A, whole animal, NMSZ 2002037.026, submature ♀, [31] mm ML. B, hectocotylus, NMSZ 2003152.004, mature ♂, 34 mm ML, scale bar = 5 mm. C, diagrammatic representation of extent of papillae and chromatophores: leu, leucophores.

with up to 33 suckers. Penis diverticulum coiled. Spermatophores long (SpLI 124.3 ± 8.6) and slender. Mature ovarian eggs large (> 10 mm). Ink sac present. Anal flaps present. Radula with nine elements, rachidian multicuspid, cusps small, may appear unicuspid when worn (Fig. 10H). Other features of digestive and reproductive systems greatly resemble those of *P. charcoti*.

Papillae appear simple and round when viewed with the naked eye. They apparently resemble those of *P. aequipapillae* or *P. aurata*, although when viewed under the microscope they are slightly less regular in structure (Fig. 9H). The papillae cover the entire dorsal surface but stop abruptly at the lateral fold (Fig. 8C). The lateral fold is marked posteriorly by a slightly raised ridge, itself marked with leucophores.

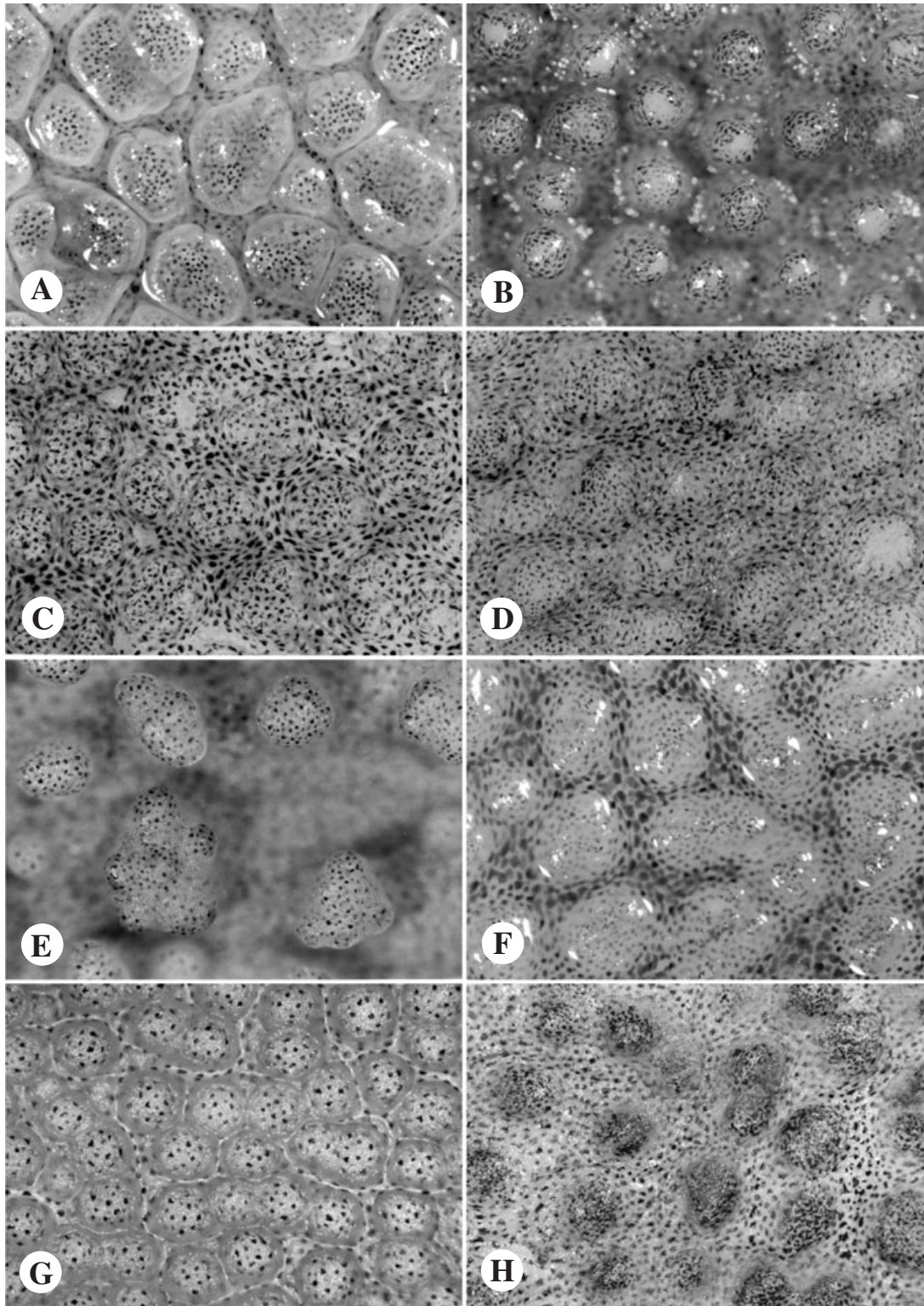


Figure 9. Papillae structure as seen under a stereomicroscope. Width of photograph encompasses 5 mm of tissue. A, *Pareledone charcoti* Joubin, 1905, NMSZ 2002037.044. B, *P. aequipapillae* sp. nov., NMSZ 2002037.004. C, *P. albimaculata* sp. nov., NMSZ 2002037.011. D, *P. aurata* sp. nov., NMSZ 2002037.003. E, *P. cornuta* sp. nov., NMSZ 2002037.018. F, *P. panchroma* sp. nov., NMSZ 2000081.051. G, *P. serperastrata* sp. nov., NMSZ 2002037.022. H, *P. subtilis* sp. nov., NMSZ 2002037.027.

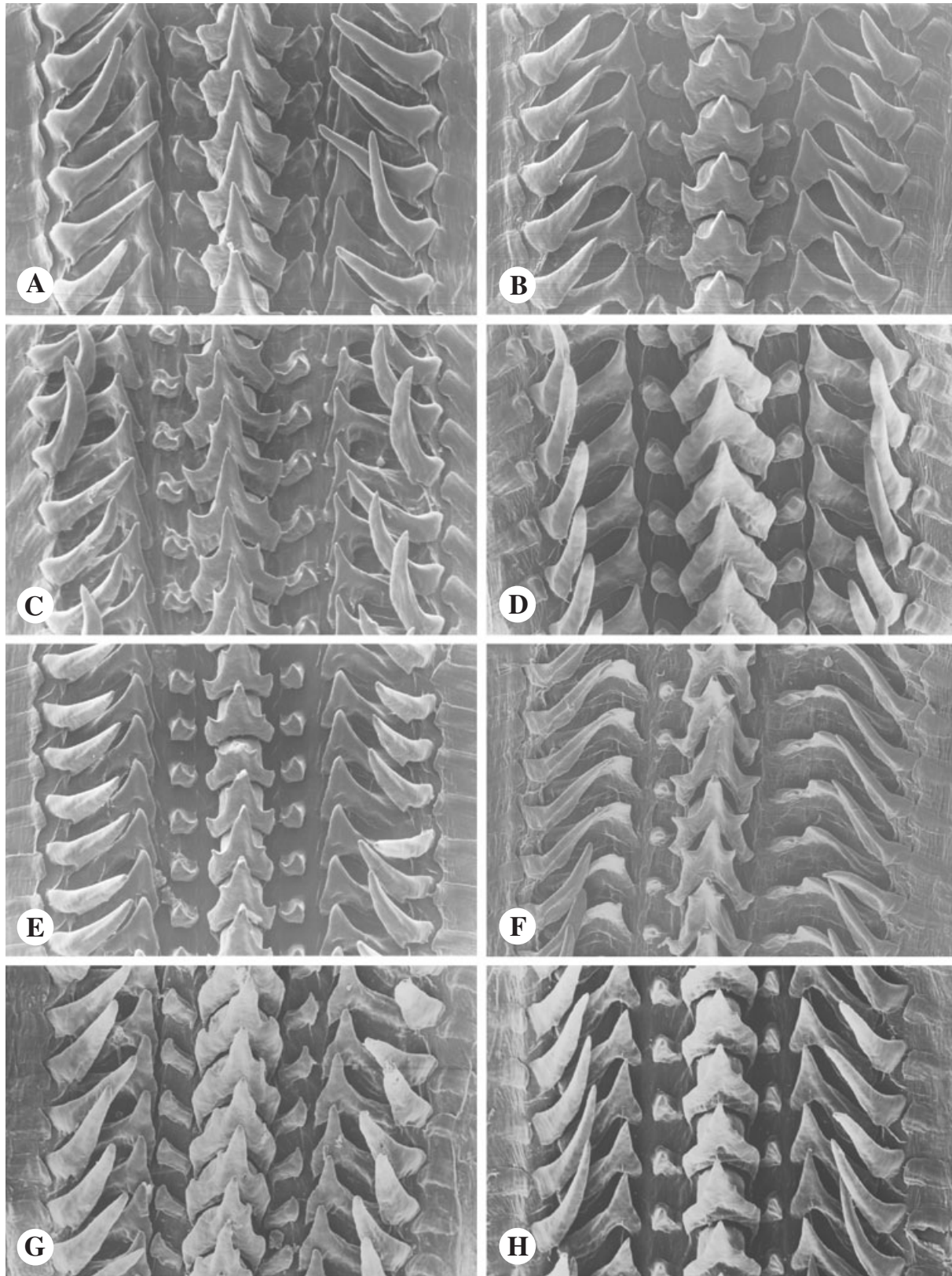


Figure 10. Radulae. A, *Pareledone charcoti* Joubin, 1905. B, *P. aequipapillae* sp. nov. C, *P. albimaculata* sp. nov. D, *P. aurata* sp. nov. E, *P. cornuta* sp. nov. F, *P. panchroma* sp. nov. G, *P. serperastrata* sp. nov. H, *P. subtilis* sp. nov.

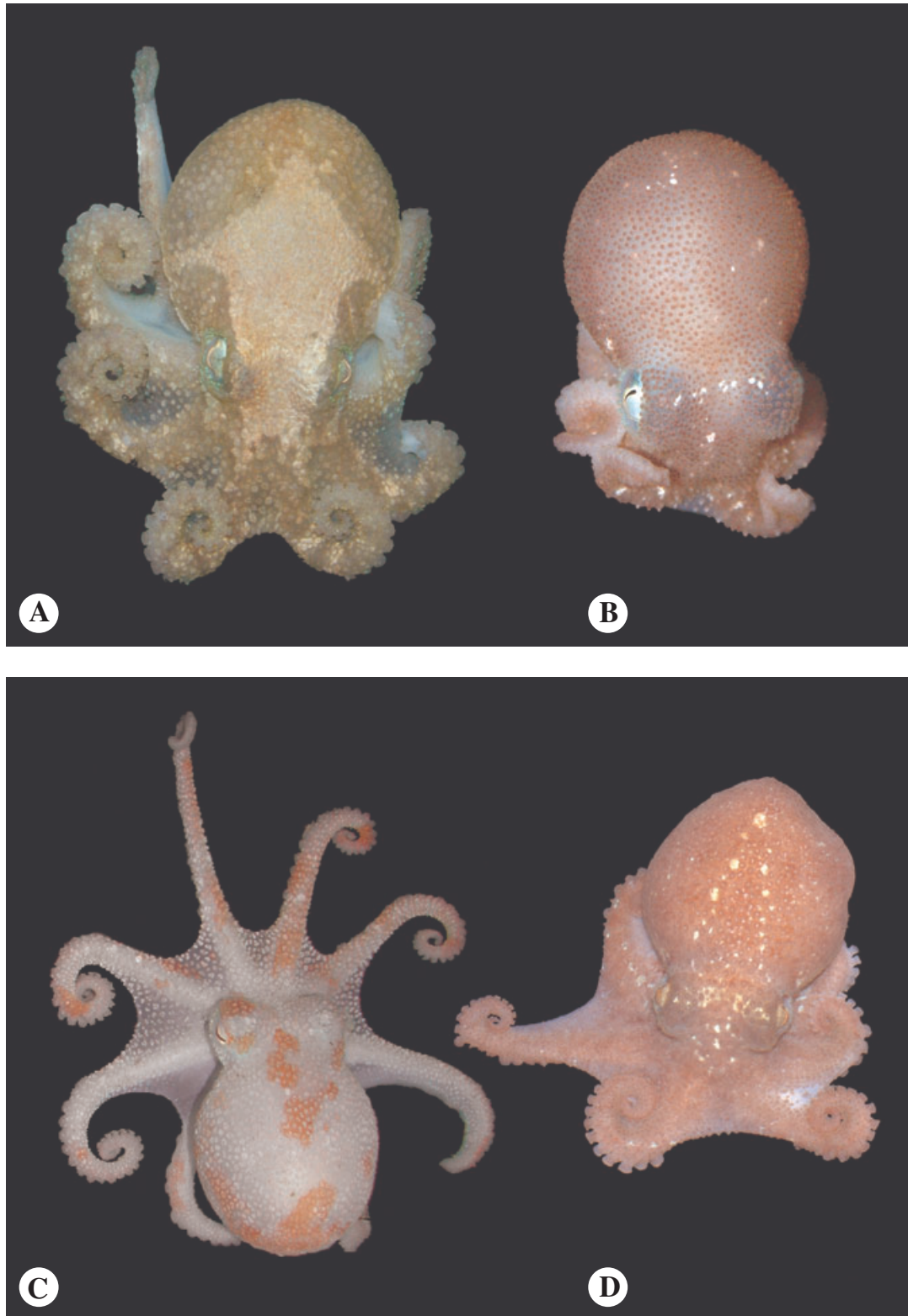


Figure 11. Live animals. A, *Pareledone charcoti* Joubin, 1905, NMSZ 2002037.044. B, *P. aequipapillae* sp. nov., NMSZ 2002037.004. C, *P. albimaculata* sp. nov., NMSZ 2002037.011. D, *P. aurata* sp. nov., NMSZ 2002037.003. E, *P. cornuta* sp. nov., NMSZ 2002037.018. F, *P. panchroma* sp. nov., NMSZ 2000081.051. G, *P. serperastrata* sp. nov., NMSZ 2002037.022. H, *P. subtilis* sp. nov., NMSZ 2002037.027.

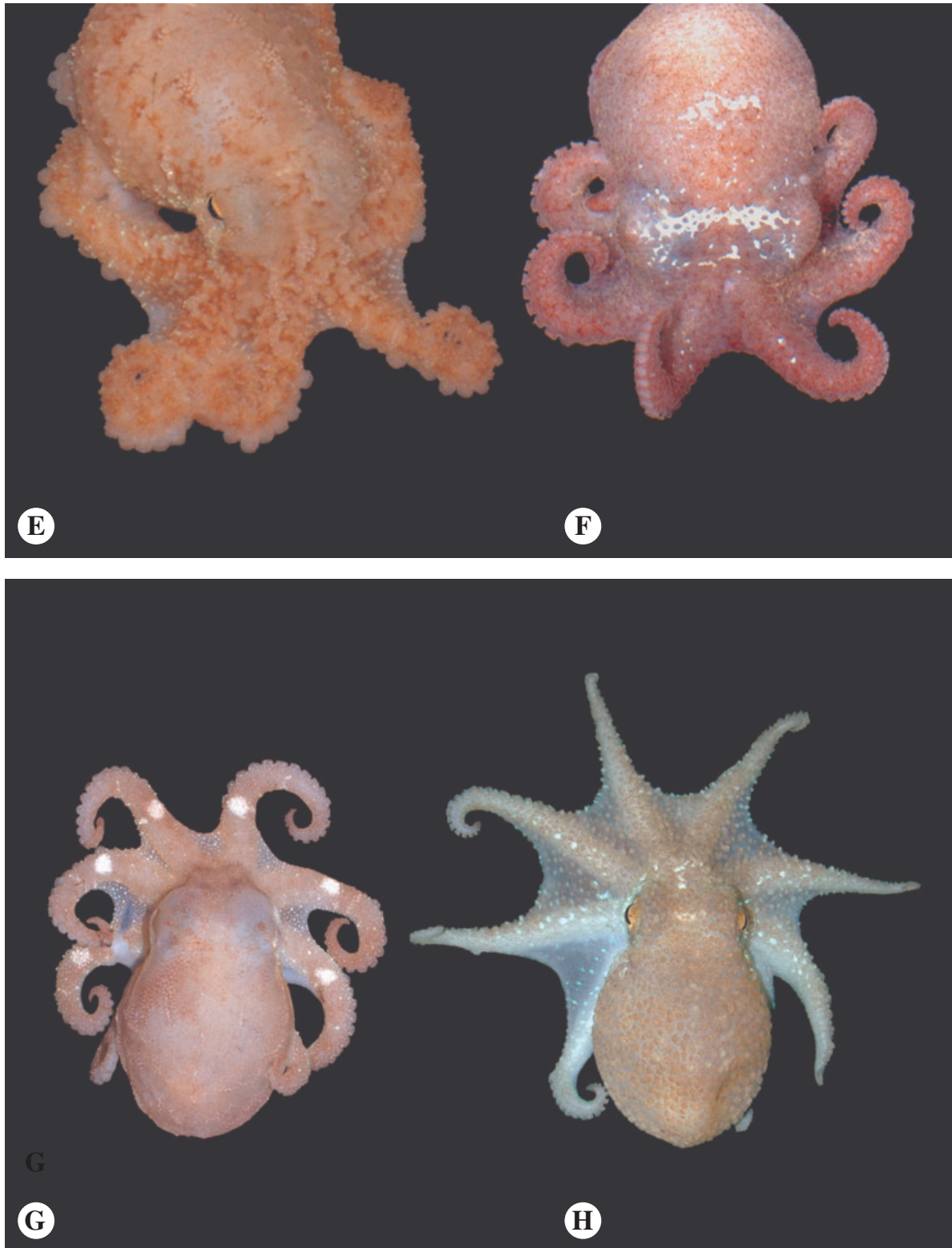


Figure 11. *Continued*

Table 8. Raw measurements from specimens of *Pareledone subtilis* used in description. All measurements in mm. *Abbreviations:* m/l, medial/lateral; l/r, left/right; d/damaged

Status	paratype		paratype		paratype		holotype		paratype		paratype	
	NMSZ	mature	NMSZ	mature	NMSZ	mature	NMSZ	mature	NMSZ	mature	NMSZ	mature
Repository	2002037.027	♀	2002037.027	♂	2002037.026	♀	2002037.026	♂	2002037.026	♀	2002037.026	♂
Catalogue number	2002037.027	♀	2002037.027	♂	2002037.026	♀	2002037.026	♂	2002037.026	♀	2002037.026	♂
Sex	♀		♂		♀		♂		♀		♂	
Maturity	mature		mature		mature		mature		mature		mature	
Total length	107		84		105		99		102		93	
Mantle length (dorsal)	39		31		39		34		35		36	
Mantle length (ventral)	36		28		36		34		34		33	
Mantle width	35		30		36		32		33		34	
Head width	23		22		24		21		23		22	
Pallial aperture	22		19		22		16		22		22	
Full funnel length	17		17		18		15		18		17	
Free funnel length	8		9		9		7		8		8	
Funnel organ length (m/l)	10/10		9/9		10/10		9/9		13/13		10/10	
Funnel organ shape	w		w		w		w		w		w	
Web depth sector A	20		12		20		12		22		20	
Web depth sector B (l/r)	21/20		15/16		21/21		16/17		23/22		21/21	
Web depth sector C (l/r)	22/22		17/17		21/19		21/17		22/24		20/21	
Web depth sector D (l/r)	21/23		17/15		21/19		21/17		21/22		15/17	
Web depth sector E	18		14		12		9		17		11	
Arm length L1	47		46		d		d		51		49	
Arm length L2	51		46		52		52		54		49	
Arm length L3	d		46		53		54		52		49	
Arm length Hc			43				50					
Arm length L4	56		46		d		56		d		44	
Sucker count Hc			24				24				24	
Sucker count L3			30		32		32		30		32	
Sucker diameter	3		2		3		2.5		2.5		2.5	
Arm width	5		3.5		5		4.5		4.5		4.5	
Ligula length			4				4.5				4.5	
Calamus length			2				2.5				2.5	
Gill lamellae: inner (l/r)	7/7		7/7		6/6		6/6		6/6		8/7	
Gill lamellae: outer (l/r)	7/7,		7/7		6/6		6/6		6/6		7/7	
Gill length (l/r)	11/12		8/9		9/11		8/10		10/10		11/11	
Gamete length	12		36		10		42		9		7	
Gamete width	6		2		5		2		5		4	

Anteriorly (towards the pallial aperture) there is no distinct division between the dorsal and ventral mantle surfaces, except the abrupt cessation of the papillae. Chromatophores continue beyond the lateral fold

onto the surface of the ventral mantle. Here they are sparser; nonetheless they cover the entire ventral surface. There are no enlarged papillae on the dorsal mantle surface. Leucophores are apparent on and just below the head region and may also be present laterally. A freshly dead specimen usually has a purple hue. Live specimens (Fig. 11H) are usually paler.

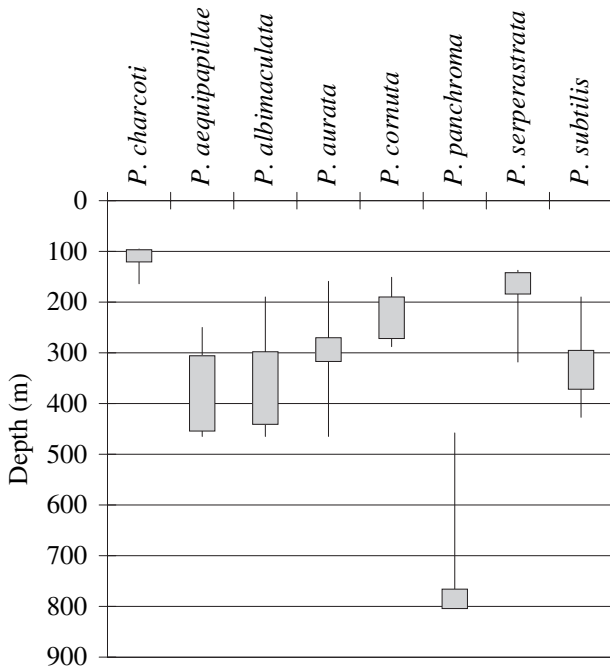


Figure 12. Depth distribution of eight species of *Pareledone*. The 5% deepest and 5% shallowest specimens of each species are excluded. Lines represent next 20% shallowest and 20% deepest specimens. Solid bars represent the middle depth bands inhabited by each species, from which 50% of specimens were captured.

Type locality

South Shetland Islands. 61°04'S, 54°37'W. 190 m. RV *Polarstern*, ANT XIX/3, Stn 61/047-1, 30.i.2002.

Distribution

South Shetland Islands, 61°04'–61°45'S, 54°34'–58°51'W, 190–427 m (this study).

Etymology

From the Latin *subtilis* (fine-spun, delicate), referring to the delicate nature of the web.

DISCUSSION

Much of the confusion surrounding *Pareledone charcoti* stems from the very different specimens lodged in the Paris Museum by Joubin under this name. The second lot, MNHN 5.7.1094, is undoubtedly a different species and is probably attributable to *P. aequipapillae* sp. nov. The difference in papillae (or tubercles as they were then referred to) was noted by Robson (1930, 1932) and commented on further by Kubodera

KEY TO IDENTIFICATION

- 1a. Pattern of modified papillae on dorsal mantle 2
- 1b. No pattern of modified papillae on dorsal mantle 6
- 2a. More than one supraocular papilla 3
- 2b. Only one supraocular papilla 4
- 3a. Papillae generally simple and round *P. aurorae*
- 3b. Papillae generally large and compound. *P. cornuta*
- 4a. Papillae stop abruptly at lateral fold *P. aequipapillae*
- 4b. Papillae coverage extends onto ventral mantle. 5
- 5a. Papillae on ventral mantle confined to edges only *P. serperastrata*
- 5b. Papillae on ventral mantle cover entire surface *P. framensis*
- 6a. Supraocular papillae present. 7
- 6b. Supraocular papillae absent 9
- 7a. Papillae round and simple *P. aurata*
- 7b. Papillae irregularly shaped. 8
- 8a. Papillae encroach onto the ventral mantle *P. albimaculata*
- 8b. Papillae do not encroach from dorsal to ventral mantle *P. charcoti*
- 9a. Ink sac absent *P. panchroma*
- 9b. Ink sac present. 10
- 10a. Papillae round and simple when viewed microscopically. *P. prydzensis*
- 10b. Papillae round and simple when viewed with naked eye but noticeably compound when viewed microscopically *P. subtilis*

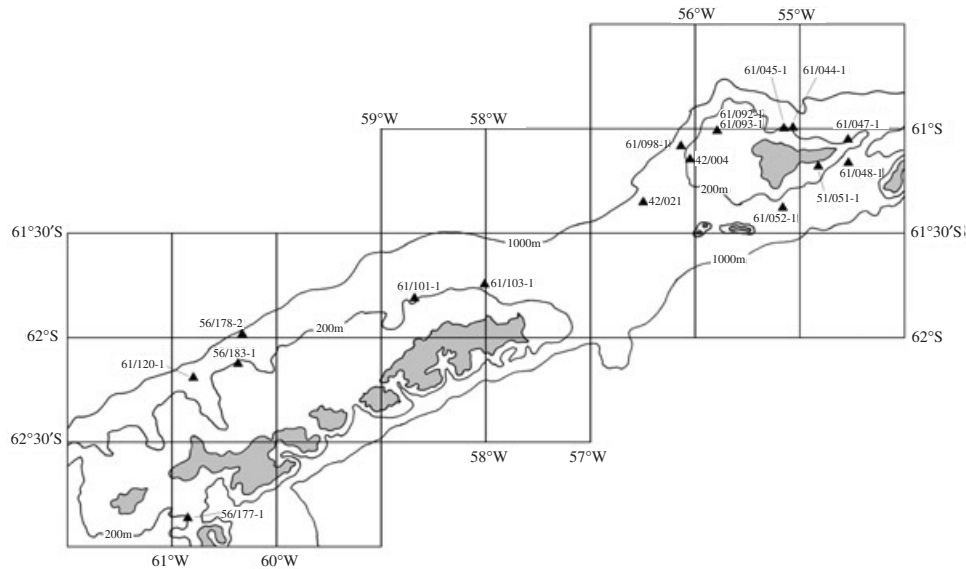


Figure 13. Locations of *RV Polarstern* stations detailed under material examined.

Table 9. A checklist of papillae characteristics for species of *Pareledone*. Y, yes; N, no

	Supraocular papillae	Papillae simple and round	Enlarged papillae on dorsal mantle	Papillae encroach on ventral mantle
<i>P. charcoti</i>	1	N	N	N
<i>P. aequipapillae</i>	1	Y	Y	N
<i>P. albimaculata</i>	1	N	N	Y
<i>P. aurata</i>	1	Y	N	anteriorly
<i>P. cornuta</i>	> 1	N	Y	Y
<i>P. panchroma</i>	0	N	N	N
<i>P. serperastrata</i>	1	Y	modified	Y
<i>P. subtilis</i>	0	with naked eye	N	N
<i>P. framensis</i>	1	Y	Y	complete cover
<i>P. prydzensis</i>	0	Y	N	N
<i>P. aurorae</i>	> 1	Y	Y	Y

& Okutani (1994). Berry (1917) noted that the 'finer' papillae of *P. aurorae* also differed from those of the holotype of *P. charcoti* by 'their farther extent ventrally'. It was only following Joubin's (1914) publication describing MNHN 5.7.1094 that Berry (1918) concluded that *P. aurorae* and *P. charcoti* may be synonymous.

In fact, it would appear that all eight species now described from the Antarctic Peninsula region differ from those described from Eastern Antarctica. *Pareledone framensis* is easily distinguished from all other species by the complete coverage of the ventral mantle with papillae. *P. prydzensis* is the only species with simple round papillae that has no enlarged supraocular papillae. *P. aurorae* is one of only two species

described to date to have more than one pair of supraocular papillae (the other being *P. cornuta*). *P. aurorae* is easily distinguished from *P. cornuta* by the very distinctive compound (branched) papillae in the latter (see Figs 5A, 9E). For a checklist of papillae characteristics in each species see Table 9.

Lu & Stranks (1994) also provide a description for *Pareledone charcoti* based on specimens from the eastern Antarctic. Their '*charcoti*' has 'fine, rounded and closely set papillae' and therefore does not fall within the newly defined bounds of the species. Examination of two of their '*charcoti*' specimens as part of this study confirms this. It is possible that their '*charcoti*' may encompass more than one species as the range of hectocotylized arm sucker counts (31–38) is much

greater than is normally seen for a single species of *Pareledone*, as is the depth range (110–683 m; cf. Fig. 12).

The redescrptions herein focus on less traditional characters, such as papillae structure and patterns, and avoid some of the more familiar characters, such as beak morphology. In this genus, as in many other octopodid genera, it does not appear possible to discern differences between the beaks of individual species, as they all show a strong resemblance to those of *Pareledone charcoti* (Fig. 1E). This is particularly frustrating to those involved in predator studies whereby prey are determined on the basis of predator gut contents. The illustration of radulae (Fig. 10) is an attempt to assist those working in this field. Although more detailed studies of radulae may be required, the present investigation shows that there are at least some differences between species, e.g. the unicuspid rachidian of *P. aurata*.

ACKNOWLEDGEMENTS

The Alfred Wegener Institute provided sea-time aboard *RV Polarstern*. Wolf Arntz, Gerhard Kattner, Karl-Hermann Kock, Uwe Piatkowski, Dieter Fütterer and others helped make this possible. Initial work was funded by a NERC CASE award to John Thorpe and Paul Rodhouse. Later work was funded by the National Museums of Scotland. The Systematics Association and the Trans-Antarctic Association provided additional funds to support the fieldwork. Mike Vecchione and Uwe Piatkowski produced the images of live octopuses and gave considerable assistance and advice while at sea. Silke Steimer also assisted at sea. Fred Naggs and Amelia MacLellan (BMNH), Melanie McKenzie and Tim Stranks (MV), Virginie Héros and Philippe Bouchet (MNHN), Ian Loch and Holly Barton (AM) and Sankurie Pye (NMSZ) provided access to specimens. Eric Hochberg critically evaluated the work and provided advice. I am particularly grateful to those who worked on *Pareledone* previously and kindly shared their knowledge.

REFERENCES

Allcock AL. 1997. The genetics and taxonomy of Southern Ocean Octopodidae, with special reference to the genus *Pareledone*. Unpublished PhD Thesis, University of Liverpool.
 Allcock AL, Hochberg FG, Rodhouse PGK, Thorpe JP. 2003. *Adelieledone*, a new genus of octopodid from the Southern Ocean. *Antarctic Science* 15 (4): 415–424.
 Allcock AL, Piatkowski U, Rodhouse PGK, Thorpe JP. 2001. A study on octopodids from the eastern Weddell Sea, Antarctica. *Polar Biology* 24: 832–838.
 Allcock AL, Piartney SB. 2002. Evolutionary relationships of Southern Ocean Octopodidae (Cephalopoda: Octopoda)

and a new diagnosis of *Pareledone*. *Marine Biology* 140: 129–135.
 Arntz WE, Brey T, eds. 2001. The expedition ANTARKTIS XVII/3 (EASIZ III) of RV ‘Polarstern’ in 2000. *Berichte zur Polar- und Meeresforschung* 402, 1–181.
 Berry SS. 1917. Cephalopoda. *Scientific Reports, Australian Antarctic Expedition, Series C, Zoology and Botany* 4 (2): 1–38.
 Berry SS. 1918. Postscript to the Cephalopoda of the Australasian Antarctic Expedition. A sheet unpagged, inserted in *Scientific Reports, Australian Antarctic Expedition, Series C, Zoology and Botany* 4 (2).
 Fütterer D, ed. 2003. The expedition ANTARKTIS XIX/3 of RV ‘Polarstern’ in 2002. *Berichte zur Polar- und Meeresforschung* 470: 1–174.
 Hoyle WE. 1912. The Cephalopoda of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 48: 273–283.
 Hoyle WE. 1910. Mollusca, Cephalopoda. In: Schultze LS, ed. *Zoologische und anthropologische Ergänzungen einer Forschungsreise in westlichen und zentralen Südafrika ausgeführt in den Jahren 1903–05*. Jena: Gustav Fischer, 261–268.
 Joubin L. 1905. Description de deux Élédones provenant de l’Expédition du Dr Charcot dans l’Antarctique. *Mémoires de la Société Zoologique de France* 18: 22–31.
 Joubin L. 1914. Cephalopodes. In: *Deuxième Expédition Antarctique Française (1908–10)*. *Science Naturelles: Documents Scientifiques*. Paris: Masson, 35–38.
 Kattner G, ed. 1998. The expedition ANTARKTIS XIV/2 of RV ‘Polarstern’ in 1996/7. *Berichte zur Polarforschung* 274.
 Kubodera T, Okutani T. 1994. Eledonine octopods from the Southern Ocean: systematics and distribution. *Antarctic Science* 6: 205–214.
 Kühl S. 1988. A contribution to the reproductive biology and geographical distribution of Antarctic Octopodidae (Cephalopoda). *Malacologia* 29: 89–100.
 Lu CC, Stranks TN. 1994. Synopsis of *Pareledone* and *Megaleledone* species, with description of two new species from East Antarctica (Cephalopoda: Octopodidae). *Memoirs of the National Museum of Victoria* 54: 221–242.
 Massy AL. 1916. Mollusca. Part. II. Cephalopoda. *British Antarctic ‘Terra Nova’ Expedition, 1910, Natural History Reports, Zoology* 2: 141–176.
 Ohdner NH. 1923. Die Cephalopoden. *Further Zoological Results of the Swedish Antarctic Expedition* 1 (4): 1–7.
 Okutani T. 1986. A note on Antarctic benthic mollusks collected with a beam-trawl from Breid Bay by the 25th Japanese Antarctic research expedition. *Memoirs of the National Institute for Polar Research, Tokyo, Special Issue* 40: 277–287.
 Piatkowski U, Allcock L, Hevia M, Steimer S, Vecchione M. 1998. Cephalopod ecology. In: Kattner G, ed. The expedition ANTARKTIS XIV/2 of RV Polarstern. *Berichte zur Polarforschung* 274, 41–47.
 Piatkowski U, Allcock L, Vecchione M. 2003. Cephalopod diversity and ecology. *Berichte zur Polarforschung* 470: 32–38.

- Robson GC. 1930.** Cephalopoda. I. Octopoda. *Discovery Reports* **2**: 371–402.
- Robson GC. 1932.** *A monograph of the recent Cephalopoda based on the collections in the British Museum (Natural History). Part II. The Octopoda (excluding the Octopodinae).* London: British Museum.
- Roper CFE, Voss GL. 1983.** Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria* **44**: 13–27.
- Taki I. 1961.** On two new eledonid octopods from the Antarctic Sea. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University* **3**: 297–316.
- Thiele J. 1920.** Die Cephalopoden der Deutschen Südpolar Expedition 1901–03. *Deutsche Südpolar Expedition [1905–31] (Zoology)* **8** (4): 431–466.
- Thore S. 1945.** On the Cephalopoda of Professor O. Carlgren's expedition to South Africa in 1935. *Kungliga Fysiografiska Sällskapet I Lund, Förhandlingar* **15** (7): 49–57.
- Voss GL. 1988.** The biogeography of the deep-sea Octopoda. *Malacologia* **29**: 295–307.
- Yau C, Allcock L, Daly HI, Collins MA. 2002.** Distribution of *Pareledone* spp. (Octopodidae: Eledoninae) around South Georgia. *Bulletin of Marine Science* **71** (2): 993–1002.